
A PHYLOGENETIC ANALYSIS OF THE *CASCABELA*–*THEVETIA* SPECIES COMPLEX (PLUMERIEAE, APOCYNACEAE) BASED ON MORPHOLOGY¹

Leonardo O. Alvarado-Cárdenas² and
Helga Ochoterena²

ABSTRACT

A parsimony cladistic analysis based on 55 morphological characters was performed for the *Cascabela* Raf.–*Thevetia* L. species complex (Apocynaceae), including 22 terminals, sampling at least one species of each genus in Plumerieae sensu Endress and Bruyns. The consensus of the 12 most parsimonious trees (length = 164, consistency index = 0.50, retention index = 0.75) can be correlated to three previous subtribal classifications. The topology supports the monophyly of the *Cascabela*–*Thevetia* species complex, but it is not conclusive to whether *Cascabela* should be recognized as a genus or as a subgenus of *Thevetia*. Because there are two important and easy-to-diagnose characters supporting each clade (digitiform supracarpal appendages and embryos not compressed in *Cascabela*; reniform fruits and segmented endocarp in *Thevetia*), the recognition of two genera is preferred here. Therefore, the new combination *C. pinifolia* (Standl. & Steyerl.) Alvarado-Cárdenas & Ochot.-Booth is proposed. Keys and synoptic descriptions for the two genera and their species are provided.

Key words: Apocynaceae, *Cascabela*, *Cerbera*, *Cerbereae*, morphology, Plumerieae, *Thevetia*, Thevetiinae.

The Apocynaceae s.l. family have approximately 5000 species and 395 genera classified in five subfamilies (Endress & Bruyns, 2000; Endress, 2004), of which Rauvolfioideae is the most diverse and heterogeneous, with 10 tribes. Among these tribes, the circumscription of Plumerieae has changed according to several authors (Table 1), and Endress and Bruyns (2000) proposed the most recent tribal classification, based on morphology and recent DNA phylogenetic hypotheses. According to this classification, Plumerieae consists of 11 genera (Endress & Bruyns, 2000; Sennblad & Bremer, 2002) including *Cascabela* Raf., *Cerbera* L., and *Thevetia* L. These genera share a close morphological relationship, which is reflected in the recognition by some authors (Lippold, 1980; Alvarado-Cárdenas, 2003) of a generic complex with an intricate taxonomic history. This begins with Tournefort (1700), who first applied the name *Ahouai* Tourn. for *T. ahouai* (L.) A. DC. Later, in the works *Genera Plantarum* and *Hortus Cliffortianus*, and *Opera Varia* Linnaeus (1737a, 1737b, 1758, respectively) changed *Ahouai* to *Thevetia*, in honor of the French monk A. Thevet. However, in

subsequent editions of *Species Plantarum* (Linnaeus, 1753) and *Genera Plantarum* (Linnaeus, 1754), Linnaeus included *Thevetia* within *Cerbera*, starting the confusion regarding the generic circumscription and creating disagreements among subsequent authors. Throughout the history of this generic complex, several names are involved, including *Ahouai* Mill. (Miller, 1751) and *Thevetia* Adans. (Adanson, 1763), and later *Plumeriopsis* Rusby & Woodson (Woodson, 1937) and *Ahorai* Pichon (Pichon, 1948a), but none of these names were correctly applied, as discussed in the taxonomic revision of *Thevetia* by Lippold (1980). After this work, the complex was divided into three genera, based on fruit characters and flower differences (Fig. 1), but Lippold's position is still in question. The long controversy includes two principal proposals: (1) to recognize *Thevetia* as different from *Cerbera*, but not from *Cascabela* (Gensel, 1969; Williams, 1996a, b; Allorge, 1998; Morales, 2005); and (2) to recognize three generic entities: *Cascabela*, *Cerbera*, and *Thevetia* (Rafinesque-Schmaltz, 1838; Lippold, 1980; Gentry, 1998; Potgieter & Albert, 2001; Alvarado-Cárdenas,

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²Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apdo. Postal 70-367, México DF 04510, México, helga@ibiologia.unam.mx.

Table 1. Different proposals of classification for the taxa that were classified within Rauvolfioideae, Plumerieae by Endress and Bruyns (2000). In all the proposals, *Cascabela* is considered as a synonym of *Thevetia*. NI = not included.

Genera	Authors					
	Endlicher (1838)	de Candolle (1844)	Schumann (1897)	Pichon (1948a, b, 1950a)	Leeuwenberg (1983, 1994)	Sennblad & Bremer (2002)
<i>Allamanda</i> L.	Subordo-1 Carisseae	Willughbeieae Allamandaeae	Plumerioideae Arduineae Landolphiineae	Plumerioideae Allamandaeae	Plumerioideae Allamandaeae	Rauvolfioideae Plumerieae
<i>Anechites</i> Griseb.	NI	NI	Plumerioideae Plumerieae Rauwolffiineae	Plumerioideae Rauvolffieae Anechitinae	Plumerioideae Rauvolffieae Anechitinae	Rauvolfioideae Plumerieae
<i>Cameraria</i> L.	NI	Plumerieae Tabernaemontanineae	Plumerioideae Plumerieae Alstoniineae	Cerbereoideae Thevetieae Camerariinae	Plumerioideae Cerbereae	Rauvolfioideae Plumerieae
<i>Cascabela</i> Raf.	Subordo-2 Ophioxyleae	Carissaeae Thevetieae	Plumerioideae Plumerieae Cerberiineae	Cerbereoideae Thevetieae Thevetiinae	Plumerioideae Cerbereae	NI
<i>Cerbera</i> L.	Subordo-2 Ophioxyleae	Plumerieae Tabernaemontanineae	Plumerioideae Plumerieae Cerberiineae	Cerbereoideae Thevetieae Cerberinae	Plumerioideae Cerbereae	Rauvolfioideae Plumerieae
<i>Cerberiopsis</i> Vieill. ex Pancher & Sebert	NI	NI	Plumerioideae Plumerieae Cerberiineae	Cerbereoideae Thevetieae Cerberinae	Plumerioideae Cerbereae	NI
<i>Himatanthus</i> Willd. ex Roem. & Schult.	NI	NI	NI	Plumerioideae Plumeriinae	Plumerioideae Plumeriinae	NI
<i>Mortoniella</i> Woodson	NI	NI	NI	Plumerioideae Plumeriinae	Plumerioideae Plumeriinae	NI
<i>Plumeria</i> L.	Subordo-3 Euapocyneae Plumerieae	Plumerieae Tabernaemontanineae	Plumerioideae Plumerieae Alstoniineae	Plumerioideae Plumeriinae	Plumerioideae Plumeriinae	Rauvolfioideae Plumerieae
<i>Skytanthus</i> Meyen	NI	Echiteae	Plumerioideae Plumerieae Plumerieae Alstoniineae	Cerbereoideae Skytanthaeae Skytanthaeae	Plumerioideae Cerbereae Cerbereae	NI
<i>Thevetia</i> L.	Subordo-2 Ophioxyleae	Carissaeae Thevetieae	Plumerioideae Plumerieae Cerberiineae	Cerbereoideae Thevetieae Thevetiinae	Plumerioideae Cerbereae	Rauvolfioideae Plumerieae



Figure 1. Exemplar species belonging to the *Cascabela*–*Thevetia* complex. —A, B. *Cascabela thevetioides*. —C. *C. gaumeri*. —D. *C. thevetia*. —E, F. *Thevetia ahouai*.

2003; Alvarado-Cárdenas & Ochoterena, 2005). Not recognizing *Thevetia* as a different genus from *Cascabela*, Williams (1996a) elevated *T. peruviana* K. Schum. in Engl. & Prantl var. *pinifolia* Standl. & Steyerl. ex Leavenw. (Leavenworth, 1946) to species rank. Therefore, eight species are currently recognized within *Thevetia* (including *Cascabela*), with six within *Cerbera*. Despite the recent cladistic analyses to classify the family and the tribe based on morphology and/or molecular data (Endress et al., 1996; Sennblad & Bremer, 1996, 2002), these works have not included all the species in the complex; they instead focused on broader questions, leaving aside the problematic circumscription of *Cascabela* and *Thevetia*.

The objective of this work is to provide evidence based on a morphological phylogenetic study for a more natural classification of the generic complex. Also, the intention is to postulate hypotheses for the relationships among the species within the species complex and to test the position of the genera within the tribe. At the same time, the results of this analysis will allow for the postulation of hypotheses for the evolution of flower and fruit characters related to pollination and dispersal syndromes. A key and synoptic descriptions of the taxa in the complex are provided to facilitate future taxonomic work.

MATERIAL AND METHODS

An intensive bibliographic compilation (monographic and floristic treatments, phylogenetic studies,

etc.) was assembled to define the species sampling, as well as to compare the observations and coding of the morphological character set: Allorge (1998); Alvarado-Cárdenas (2003, 2004); Boiteau & Allorge (1978); Endress (1996); Endress & Bruyns (2000); Endress et al. (1983, 1996); Ezeurra (1981); Fallen (1983, 1984, 1985, 1986); Gensel (1969); Gentry (1998); Leeuwenberg (1983, 1994, 1999); Nilsson (1986, 1990); Nowicke (1970); Pichon (1948a, b, 1949, 1950a, b); Pire (1989); Plumel (1991); Potgieter & Albert (2001); Rosatti (1989); Roubik & Moreno (1991); Rzedowski & Rzedowski (1998); Sennblad & Bremer (1996, 2002); Sennblad et al. (1998); Simoes & Kinoshita (2002); Standley (1924); Standley & Williams (1958); Veillon (1971); Williams (1996a, b, 2002); Woodson (1935, 1938a, b); and Woodson & Moore (1938).

TAXON SAMPLING

Twelve genera and 22 species were included in the cladistic analysis (Table 2). This sampling includes for the first time all species of *Cascabela* (four species) and *Thevetia* (four species), three representative species of *Cerbera* (out of six), and at least one species of each genus within Plumerieae sensu Endress and Bruyns (2000). *Carissa macrocarpa* (Eckl.) A. DC. was used as the functional outgroup according to Sennblad and Bremer (1996), who suggested that it is a member of the sister tribe Carissae (*Carissa* L. and *Acokanthera* G. Don f.). This outgroup was also selected considering potential

Table 2. List of genera and species included in the analysis.

Genera	Species total/included	Species
<i>Carissa</i>	30/1	<i>C. macrocarpa</i> A. DC.
<i>Allamanda</i>	14/1	<i>A. cathartica</i> L.
<i>Anechites</i>	1/1	<i>A. nerium</i> (Aubl.) Urb.
<i>Cameraria</i>	3/1	<i>C. latifolia</i> L.
<i>Cascabela</i>	4/4	<i>C. gaumeri</i> (Hemsl.) Lippold <i>C. ovata</i> (Cav.) Lippold <i>C. thevetia</i> (L.) Lippold <i>C. thevetioides</i> (Kunth) Lippold
<i>Cerbera</i>	6/3	<i>C. floribunda</i> K. Schum. <i>C. odollam</i> Gaertn. <i>C. manghas</i> L.
<i>Cerberiopsis</i>	3/1	<i>C. candelabra</i> Vieill. ex Pancher & Sebert
<i>Himatanthus</i>	13/1	<i>H. obovatus</i> (Müll. Arg.) Woodson
<i>Mortoniella</i>	1/1	<i>M. pittieri</i> Woodson
<i>Plumeria</i>	7/2	<i>P. obtusa</i> L. <i>P. rubra</i> L.
<i>Skytanthus</i>	2/2	<i>S. acutus</i> Meyen <i>S. hancorniaefolius</i> (A. DC.) Miers
<i>Thevetia</i>	4/4	<i>T. ahouai</i> (L.) A. DC. <i>T. amazonica</i> Ducke <i>T. bicornuta</i> Müll. Arg. <i>T. pinifolia</i> (Standl. & Steyerf.) J. K. Williams

inclusive synapomorphies, as proposed by Nixon and Carpenter (1994).

CHARACTER SAMPLING

The homology hypotheses represented by the character and character state definitions follow the conjunction and similarity (position, form, and function) criteria of Patterson (1982) and De Pinna (1991). Floral and vegetative macromorphological structures were studied from personal collections and more than 900 sheets from herbarium material listed in Appendices 1 and 2. The specimens are deposited in the following herbaria: G, MEXU, MO, NY, SP, XAL, and Z. Reproductive characters were studied from the spirit material and flower anatomical section slide collections of M. Endress at Z.

Pollen grains and floral structures observed under a scanning electron microscope (SEM; Hitachi S-2460N) at the Institute of Biology, UNAM were dehydrated and covered with gold-palladium inside an ionized camera (Emitech K550). Pollen grains for observation under optic microscopy were acetolyzed following Erdtman (1960) and mounted on slides using glycerin. At least 20 grains per species were measured at polar and equatorial axis lengths. The pollen and floral structures were sampled with the authorization of their respective herbaria (MEXU, MO, NY). Sampled collections are indicated by a dagger (†) in Appendix 2.

The following continuous characters were analyzed using descriptive statistics to define the character states: bract length (7), sepal length (9), and pollen diameter (22). Species-level box graphs were constructed from all of the specimen measurements, considering standard error and deviation, using the program Statistica V.6.0.3 (not shown, available from the authors; Statsoft Corporation, Tulsa, Oklahoma). The intervals, which correspond to the proposed character states, were defined to reduce overlap of standard deviation.

PHYLOGENETIC ANALYSIS

A morphological matrix (Table 3) was constructed and edited in WinClada (Nixon, 2002), and analyzed using NONA (Goloboff, 1999). To find the most parsimonious trees (MPTs), heuristic searches using tree bisection-reconnection (TBR) were conducted with 2000 replications (in sets of 1000) using different starting trees (Wagner trees built with random addition sequences), holding 20 trees on each replication. The searches were followed by a more extensive TBR holding up to 50,000 trees (twice: h50,000; h/20; mu*1000; max*; sv*). Branches with ambiguous support in the MPTs were collapsed, identical trees were removed, and a consensus tree was calculated using the option “Consensus (strict)” in WinClada and saved as a metafile edited in Adobe Photoshop 6.0. The option “apo[” of NONA (Goloboff,

Table 3. Morphological matrix used in the analysis. Characters and character states as in Appendix 3. Ambiguity key: inapplicable = -; missing data = ?; polymorphism A = 0, 1, B = 1, 2. Generic key: A = *Allamanda*, An = *Anechites*, C = *Cameraria*, Ca = *Carissa*, Cas = *Cascabela*, Ce = *Cerbera*, Cerb = *Cerberiopsis*, H = *Himatanthus*, M = *Mortoniella*, P = *Plumeria*, S = *Skytanthus*, T = *Theretia*.

	0	5	10	15	20	25	30	35	40	45	50
<i>Ca. macrocarpa</i>	1	1	1	1	1	1	1	1	1	1	1
<i>P. rubra</i>	2	2	2	2	2	2	2	2	2	2	2
<i>P. obtusa</i>	2	2	2	2	2	2	2	2	2	2	2
<i>H. obovatus</i>	2	2	2	2	2	2	2	2	2	2	2
<i>M. pittieri</i>	2	2	2	2	2	2	2	2	2	2	2
<i>A. anthracina</i>	1	2	2	2	2	2	2	2	2	2	2
<i>S. acutus</i>	1	0	A	1	0	0	1	0	0	1	1
<i>S. hancorniaefolius</i>	1	0	B	A	1	0	0	0	0	1	1
<i>An. nerium</i>	0	1	1	0	0	1	1	0	1	0	0
<i>C. latifolia</i>	1	1	0	0	0	0	0	0	1	0	1
<i>Cerb. candelabra</i>	2	2	1	1	1	1	1	1	1	1	1
<i>Ce. odollam</i>	2	2	0	1	1	1	1	1	1	1	1
<i>Ce. floribunda</i>	2	2	0	1	1	1	1	1	1	1	1
<i>Ce. manghas</i>	2	2	0	1	1	1	1	1	1	1	1
<i>L. laevis</i>	1	0	1	2	1	0	1	1	1	1	1
<i>L. amazonica</i>	1	0	1	2	1	0	1	1	1	1	1
<i>T. pinnifolia</i>	B	0	1	1	0	1	0	1	1	1	1
<i>T. ahouai</i>	B	0	1	1	A	0	0	1	1	1	1
<i>Cas. nana</i>	2	2	1	0	1	0	1	0	1	0	1
<i>Cas. gaumeri</i>	2	2	0	1	0	1	0	1	0	1	0
<i>Cas. thevetioides</i>	2	0	0	1	0	1	0	1	0	1	0
<i>Cas. thevetia</i>	2	0	0	1	0	1	0	1	0	1	0

1999) was used to identify the character states that unambiguously support the branches of the consensus in all MPTs. With this option, the potential artifacts that result from mapping characters onto the collapsed branches of a consensus (Nixon & Carpenter, 1996) are corrected. To evaluate the relative stability of clades in the consensus, a character removal analysis (Davis et al., 1993), as applied in Luna and Ochoterena (2004), was conducted using NONA (Goloboff, 1999) enabled through the corresponding option in WinClada (Nixon, 2002), using the same parameters as for the original matrix. The goal of this analysis was also to evaluate the contribution of individual characters to the topology of the consensus in order to postulate strategies for future research.

RESULTS AND DISCUSSION

A total of 55 potentially informative characters were included in the matrix (Table 3); 22 are multistate and six of them (1, 7, 9, 22, 33, 54) were coded as additive (cf. Appendix 3). The matrix has a total of 1210 cells, with eight (0.6%) of them coded as missing (?) and 75 (6.1%) as inapplicable (-).

The heuristic search yielded 12 MPTs (length (L) = 164, consistency index for entire tree (CI) = 0.50, retention index (RI) = 0.75), the consensus of which (Fig. 2; L = 174, CI = 0.47, RI = 0.72) recovers two main clades. The main hierarchical groups correlate to the three taxa proposed by Pichon (1948b, 1950a) and Leeuwenberg (1983, 1994): (1) Plumeriinae,

represented here by *Himatanthus* Willd. ex Roem. & Schult., *Mortoniella* Woodson, and *Plumeria* L.; (2) Allamandaeae, represented by *Allamanda* L., and (3) Cerbereae, represented by the remaining genera. Based on the proposal of Endress and Bruyns (2000), we suggest adjusting these proposed groups to the rank of subtribes, which by nomenclatural priority would be Plumeriinae, Allamandinae, and Thevetiinae (Table 1; Fig. 2).

ALLAMANDA

The position of *Allamanda* as sister to Thevetiinae (supported by shape of the upper extension of the connective [character 19/state 1, cf. Appendix 3; consistency index for character (ci) = 0.66], presence of infrastaminal appendages [27/1, ci = 0.50], and receptivity pattern type 1 [39/1, ci = 1.0]) conflicts with the hypotheses based on molecular data (Sennblad & Bremer, 1996) and combined analyses (Endress et al., 1996; Potgieter & Albert, 2001). In those analyses, species of *Allamanda* form the most inclusive clade, sharing a most recent common ancestor with *Himatanthus* and *Plumeria*. These conflicting results reflect the morphological complexity of *Allamanda* and its 14 species, and reinforce the need to continue investigating its phylogenetic position. Provisionally, our results support the recognition of a separate subtribal category for *Allamanda* (Allamandinae) as previously suggested (Pichon, 1948b; Leeuwenberg, 1983, 1994).

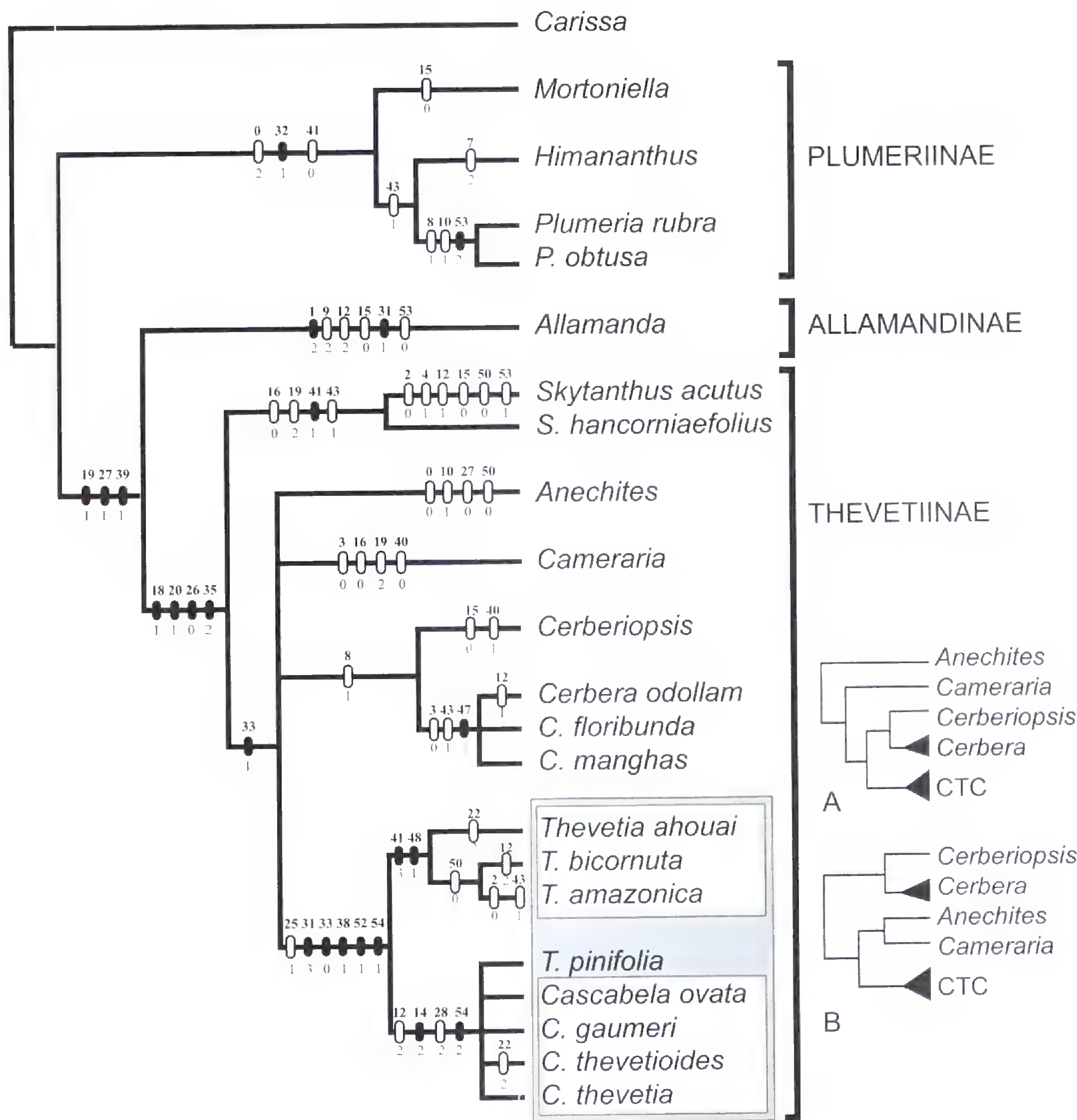


Figure 2. Consensus of 12 most parsimonious trees (MPTs, L = 164, CI = 0.50, RI = 0.75) for the members of tribe Plumerieae and the suggested subtribal classification. Solid ellipses represent synapomorphic states and hollow ones homoplasies. Only nonambiguous character states present in all MPTs are mapped onto the consensus. Numbers above the ellipses correspond to the characters and the numbers below them to the states. Inside the gray rectangle are the species classified by Gensel (1969) as *Thevetia* subg. *Thevetia* and *Thevetia* subg. *Yccotli* (*Cascabela*). Inside the white rectangles are the species considered by Lippold (1980) as belonging to *Thevetia* and *Cascabela*. A, B. Topologies found among the MPTs showing the two alternative hypotheses for the sister group of the *Cascabela–Thevetia* clade (CTC). —A. Topology that supports the traditional view. —B. Topology that supports, in part, the molecular works.

RELATIONSHIPS WITHIN SUBTRIBE PLUMERIINAE

The consensus tree supports the monophyly of Plumeriinae, which corroborates previous classifications by Pichon (1948b, 1950a), Leeuwenberg (1983, 1994), and Plumel (1991), who suggested a close relationship among *Himatanthus*, *Mortoniella*, and *Plumeria*. Plumeriinae is supported as monophyletic by these characters: life form (0/2, ci = 0.50); ovary position (32/1, ci = 1.0); and shape of non-

compressed fruits (41/0, ci = 0.75). Our results also corroborate Potgieter and Albert (2001), where *Plumeria* and *Himatanthus* are also sister.

RELATIONSHIPS WITHIN SUBTRIBE THEVETIINAE

Thevetiinae is supported as monophyletic by having the anther dehiscence latrorse (18/1, ci = 1.0), a dark apical connective color (20/1, ci = 1.0), absence of a depression in the mesocolpium (26/0, ci = 1.0), and

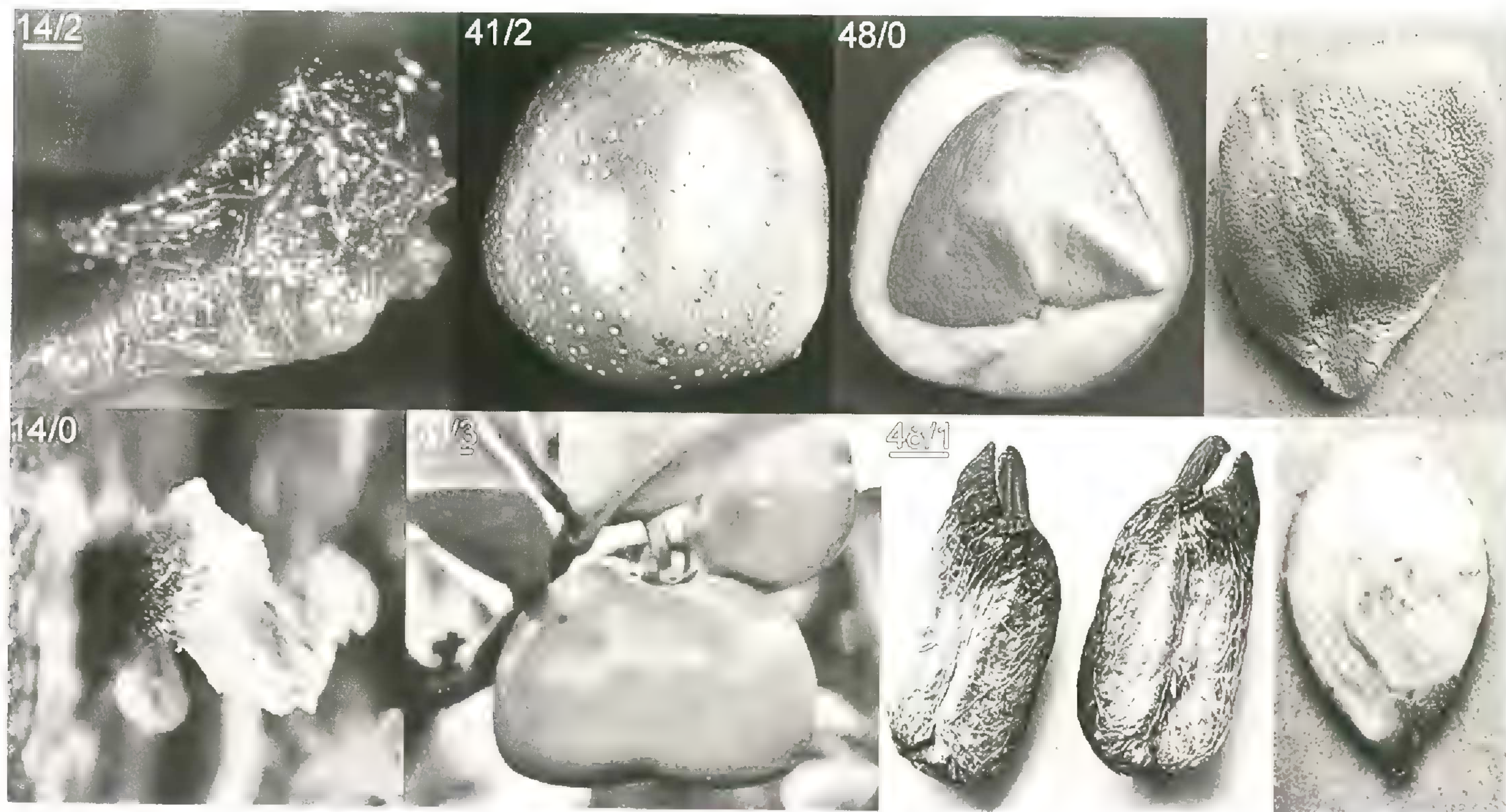


Figure 3. Characters/character states (see Appendix 3) that support the monophyly of *Cascabela* (upper row) and *Thevetia* (lower row). The underlined numbers indicate synapomorphic states that support the corresponding genera.

conical stigmata (35/2, $ci = 1.0$). These characters were previously used to circumscribe the elements of the subfamily Cerberioideae (Pichon, 1948a; Fallen, 1983).

Skytanthus Meyen was resolved as monophyletic, supported by the combination of sessile anthers (16/0, $ci = 0.50$), a filamentous upper extension of the connective (19/2, $ci = 0.66$), fusiform fruits (41/1, $ci = 0.75$), and lenticels on the exocarp (43/1, $ci = 0.20$). The position of this genus as the earliest derived within the subtribe is somewhat in agreement with Pichon (1948a), who suggested the genus as the most primitive within his subfamily Cerberioideae.

Phylogenetic relationships of the Cascabela–Thevetia species complex. Within subtribe Thevetiinae, three clades correspond more or less to *Cascabela*, *Cerbera*, and *Thevetia*, but *Cascabela* is resolved as paraphyletic, because *T. pinifolia* (Standl. & Steyerf.) J. K. Williams is nested with four other species of *Cascabela*. There is still no consensus regarding the question of whether one should recognize one genus with two subgenera (Gensel, 1969) or two distinct genera (Lippold, 1980), given that *Cascabela* and *Thevetia* are sister taxa (Fig. 2). Nevertheless, based on the unique combination and the clear contrast of character states (Fig. 3), we support the recognition of two genera: *Cascabela*, with two synapomorphies (digitiform supracarpal appendages [14/2, $ci = 0.6$]; embryos not compressed [54/2, $ci = 1.0$]), and *Thevetia*, also with two synapomorphies (reniform fruits [41/3, $ci = 0.75$];

segmented endocarp [48/1, $ci = 1.0$]). Thus, we propose a new combination for *T. pinifolia* as *Cascabela* (see Appendix 4).

The relationship of *Cascabela* and *Thevetia* as sister taxa is in disagreement with the phylogeny presented by Potgieter and Albert (2001), where *T. ahouai* shared a most recent common ancestor with *Pteralyxia kauaiensis* Caum, while *T. peruviana* (Pers.) K. Schum. (= *Cascabela thevetia* (L.) Lippold) is sister to *Amsonia* Walter. Nevertheless, in our analysis, the sister relationship of these genera is strongly supported by five synapomorphies: partial syncarpy (31/3, $ci = 1.0$), two ovules per carpel (33/0, $ci = 1.0$), a secretory region cylindrical to elliptic (38/1, $ci = 1.0$), denticulate margins of the seed wing (52/1, $ci = 1.0$), and the embryo compressed on one side (54/1, $ci = 1.0$); in addition to one homoplasie character state, the presence of endofissures in the nexine (25/1, $ci = 0.50$). The discrepancy in the results by Potgieter and Albert (2001) could be explained by sampling artifacts (with only two representatives from the generic complex). Conversely, due to lack of material, our study did not include species of *Pteralyxia* K. Schum. & Prantl and *Amsonia*, and therefore future analyses should take into account these sampling issues.

Cerbera was resolved as monophyletic, supported by the absence of indumentum on vegetative parts (3/0, $ci = 0.16$), lenticels on exocarp (43/1, $ci = 0.20$), and the endocarp forming a network with the mesocarp (47/1, $ci = 1.0$). In the consensus (Fig. 2), this genus shares a most recent common ancestor with *Cerberiopsis* Vieill. ex Pancher & Sebert, supported by

having obovate sepals (8/1, $ci = 0.50$). The relationship of *Cerbera* as sister to *Cerberiopsis* restricts the generic complex to *Cascabela* and *Thevetia*. At the same time, this sister relationship contrasts with Pichon's (1948a) proposal to group *Cerberiopsis* and *Cameraria* L. within Cameriinae based on fruit compression. However, in our analysis this character appears in all MPTs twice independently (fruit strongly compressed in cross-section; 40/1, $ci = 0.50$). Our analysis corroborates Potgieter and Albert (2001), where *Cerbera* and *Cerberiopsis* are also sister taxa, as well as the observations of Leeuwenberg (1999) and Veillon (1971), who suggested a close relation between these genera based on vegetative and floral appearances.

The sister group of the *Cascabela–Thevetia* clade (hereafter named CTC) is uncertain due to the existence of two conflicting topologies among the MPTs that result in a polytomy in the consensus. Among the MPTs, one topology suggests a sister relationship of the CTC with *Cerbera–Cerberiopsis* (Fig. 2A), supported by the unique combination of obovate leaf blades (2/2, $ci = 0.33$), floral bracts 4–11.5 mm (7/1, $ci = 0.40$), and a connate apical connective (21/1, $ci = 1.0$). This resolution supports the traditional perception of Gensel (1969), Lippold (1980), and Alvarado-Cárdenas (2003). A second topology resolves *Cameraria* and *Anechites* Griseb. as sister to the CTC (Fig. 2B) and is supported by ornamentation on the infrastaminal trichomes (29/1, $ci = 0.33$); nectary (34/1, $ci = 0.33$); and a sclerified endocarp (45/1, $ci = 0.50$). These characters have never been employed to suggest relationship among genera within the tribe. Although this topology is in disagreement with tradition, it corroborates, in part, the relationship supported by molecular data (Sennblad & Bremer, 2002), which also recovered a similar clade including the four genera. According to Sennblad and Bremer (2002), *Anechites* is resolved as sister to *Thevetia*, with *Cerbera* as sister to them and *Cameraria* sharing their most recent common ancestor.

The resolution among species of *Cascabela* lacks hierarchic structure in the consensus (Fig. 2). Among the MPTs, there are three alternative topologies for their relationships, where *C. gaumeri* (Hemsl.) Lippold and *C. ovata* (Cav.) Lippold have the most variable position, placed either as the earliest or most derived species.

Character removal: Topological consensus resolution. Twenty-seven (5, 10–12, 13, 15, 17, 18, 20, 22, 23, 25, 26, 28, 31, 35–38, 42, 46, 47, 49, 51–54) out of the 55 characters can be removed without affecting the topology of the consensus.

Removing characters 3 (presence of indumentum on vegetative parts) or 4 (secondary veins) reduces conflict within the *Cascabela* clade. The topology obtained without any of these characters is the same as one of the alternative hypotheses among the original MPTs. By removing character 14 (shape of supracarpal appendages), there is an increase in resolution within the *Cerbera* clade. When removing characters 1 (phyllotaxis), 9 (sepal length), or 45 (endocarp texture), the topology of the consensus trees supports the sister relationship of *Cerbera–Cerberiopsis* and the CTC. This topology coincides with one of the alternative resolutions among the original MPTs (Fig. 2A). In contrast, when characters 7 (length of bracts), 21 (apical connective arrangement), 24 (exine thickness), 30 (infrastaminal trichomes ornamentation pattern), or 44 (mesocarp consistency) are removed, the sister relationship of the clade *Cameraria–Anechites* and the CTC is recovered (Fig. 2B). Removing characters 41 (shape of non-compressed fruits) and 48 (endocarp presentation) results in lack of support for the genus *Thevetia* as monophyletic. Nevertheless, the reniform shape of the fruits and the segmented endocarp characteristic of all species of *Thevetia* present a strong homology hypothesis supported by morphological and anatomical studies (Pichon, 1948a, 1950b; Alvarado-Cárdenas, 2003). Therefore, we are convinced of the monophyletic nature of this genus. The removal of characters 6 (presence of a dominant axis in the inflorescences that branch) or 8 (sepal shape) results in a decrease in the resolution of the consensus within the *Thevetia* clade, and the clade *Cerbera–Cerberiopsis* is collapsed.

By removing characters 0 (life form), 27 (presence of infrastaminal appendages), 32 (ovary position), 39 (receptivity pattern), or 40 (fruit shape in cross-section), the relative position of *Mortoniella* and *Allamanda* is lost, collapsing both genera to a basal polytomy. The removal of characters 2 (leaf blade shape), 16 (presence of a structure supporting the anther), 29 (presence of ornamentation on the infrastaminal trichomes), 33 (number of ovules per carpel), 34 (presence of nectary), 43 (presence of lenticels on the exocarp), or 50 (presence of a wing on the seed) results in a decrease of resolution within subtribe Cerberineae. Some of these characters are postulated as homologies with the support of careful morphological studies (e.g., character 16 (Fallen, 1986); characters 33 and 50 (Pichon, 1948a)); others should be re-evaluated considering a bigger sample size and/or alternative coding (characters 2, 29, 41, 43). The removal of character 19 (shape of the upper extension of the connective) collapses the backbone of the consensus, but the clades corresponding to the CTC, *Cerbera–Cerberiopsis*, and Plumeriinae are still

supported. This character has been used before in phylogenetic analyses (e.g., Endress et al., 1996; Williams, 2002), but here, as mentioned, we highlight its vital importance to recover the topologies of the MPTs. Because this character does not include polymorphism within taxa and its states are unambiguously defined, we recommend that future analyses that consider morphology include it to test if it is corroborated by independent evidence.

EVOLUTION OF CHARACTERS RELATED TO REPRODUCTIVE BIOLOGY AND FLORAL MORPHOLOGY

For Apocynaceae subfamily Asclepiadoideae, numerous works related to pollination biology have been published. These works report mainly species of Diptera, Hymenoptera, and Lepidoptera involved in the complex systems of pollination. In contrast, this type of information for early derived groups within the family is scarce (Lopes & Machado, 1999). For Plumerieae, there are only records for *Himatanthus* and *Plumeria*, which are pollinated by sphingids displaying a process named "pollination by deceit" (Haber, 1984; Plumel, 1991; Knudsen & Tollsten, 1993; Oliveira et al., 2004). The species of *Himatanthus* and *Plumeria* lack nectaries, but they deceive pollinators by displaying many white flowers with strong and attractive fragrances produced at the same time that other species with nectar are in flower. *Mortoniella pittieri* Woodson probably has the same pollination system, because it shares the most recent common ancestor (Fig. 2) and the same character states (Table 3) with both genera. Several species from the *Cerbera*–*Cerberiopsis* clade (hereafter referred as the CCC) also have white flowers, have strong fragrances, and lack nectaries (Leeuwenberg, 1999). Given this pollination syndrome, it is possible that they are also pollinated by sphingids, but the only evidence to suggest that they also exhibit deceit pollination is the lack of nectaries. In contrast to the flower morphology of Plumerieae, the flowers of the CCC have supstaminal and infrastaminal appendages, which may restrict the pollinators from reaching the pollen. The presence of these appendages (13/1, $ci = 0.33$) is a derived condition in all the MPTs, although the relative time of appearance is ambiguous.

Also with white flowers, *Anechites* and *Cameraria* differ from the previous genera in that they have nectaries. These structures allow us to predict that in the pollination system of both genera, there is no deceit pollination. It could be that all members of the tribe are pollinated by Lepidoptera, even those with yellow flowers (Weberling, 1989; Proctor et al., 1996) such as *Allamanda*, *Cascabela*, *Skytanthus*, or *Theretia*; nevertheless, labels of herbarium material in-

dicate that some species are visited by hummingbirds (*Cascabela ovata*: Pérez A. 861, MEXU) and bees (*C. ovata*: Lott 430, MEXU). Of all the genera with yellow flowers, only *Skytanthus* lacks nectaries. The interpretation of the evolution of nectaries (34) is ambiguous among the MPTs; in all cases, their presence is a derived condition, but in some hypotheses, their absence is plesiomorphic, whereas in others there is a secondary loss ($ci = 0.5$ – 0.33). It would be interesting to solve this ambiguity, because it may imply a relative increase in the complexity of the flowers, from flowers without nectaries or staminal appendages to flowers without nectaries but with staminal appendages to flowers with both structures.

An increase of structural complexity was suggested by Fallen (1986). She considered *Theretia* (including *Cascabela*) to be one of the most derived genera within Plumerieae, due to the presence of a lobulate secretory region to which the infrastaminal appendages adhere, forming the gynostegium. Here we can corroborate this hypothesis. Not only is the presence of staminal appendages (13/1) derived, but so is the presence of a lobulate secretory region (38/1), which appears a posteriori as a synapomorphy of one of the most derived clades, *Cascabela*–*Theretia*.

Endress (1996) suggested that the presence of appendages in the apical connective region of the anthers could be related to the pollination systems in subfamily Asclepiadoideae. Within Plumerieae, all the genera present these structures, but their shape is variable among genera. In our analysis, the obtuse shape of the anther apical connective (19/0) represents the plesiomorphic condition, which derived into the deltoid connective (19/1) that, in turn, transformed into filamentous connectives (19/2) twice independently (in *Cameraria* and *Skytanthus*). This transformation series could be interpreted as a progressive increase in the length of the connective tissue, but there is no information about the possible function of this structure, which could be involved in the pollination process.

In terms of floral complexity, there are different degrees of fusion of the carpels within the tribe. According to the MPTs, the ancestral condition for the carpel arrangement is apocarpous (31/2), which uniquely derived into secondary syncarpous (31/1) in *Allamanda* and independently also derived into partially syncarpous (31/3) in the CTC. This pattern is also present among other genera in the family, where the ancestral condition is the apocarpous that derives into syncarpous (Endress et al., 1996). One could then interpret a tendency toward fusion of the carpels within the family. In our analysis, carpel fusion (31/3) is correlated (occurs in the same internode) with lowest number of ovules per carpel (33/0). Neverthe-

less, there is a previous step in the reduction of ovule number (33/1) that is not correlated to any degree of carpel fusion.

EVOLUTION OF THE CHARACTERS RELATED TO DISPERSAL

Fallen (1985, 1986) proposed that within Plumerieae, the basic fruit type is water dispersed. The texture of the fruit (in this case of the mesocarp) and color of the exocarp, as well as the presence/absence of wings in the seed, are features that can be directly associated to dispersal. In the tribe, the mesocarp (44) can be woody, leathery, spongy, or fleshy. The interpretation of the evolution of this character in the consensus tree is ambiguous regarding the ancestral condition (woody or spongy), but in all cases fleshy and leathery fruits are always interpreted as independently derived conditions. The spongy texture, which has been associated with water dispersal (Gunn & Dennis, 1976; Ridley, 1990), could be the ancestral condition in the tribe, but it could also have appeared one to three times depending on the MPT and the optimization. At the same time, in all the MPTs, the winged seeds must be interpreted as the plesiomorphic condition, with three lost independently in *Anechites*, *Skytanthus acutus* Meyer, and *Thevetia amazonica* Ducke–*T. bicornuta* Müll. Arg. Furthermore, the compression of the seeds on both faces (54/0), which can facilitate wind dispersal, is the ancestral state. The compression of the embryo was lost in one side (54/1) in *Thevetia* and was completely lost (54/2) in *Cascabela*, suggesting that mechanisms other than anemochory are derived. In summary, our results support the hypothesis that anemochory is the ancestral mechanism of dispersion, while zoochory and hydrochory are derived within the tribe.

There are reports that *Thevetia*, with leathery mesocarp (44/1), is dispersed by animals (e.g., Fallen, 1986, reported that *T. ahouai* is consumed by monkeys), which corroborates zoochory as one of the most derived dispersal mechanisms in Plumerieae. Fleshy-colored fruits have been associated with animal dispersal (Fahn, 1982; Ridley, 1990). Although there are no reports of dispersal mechanism for species of *Cascabela*, the presence of fleshy mesocarp (44/2) with black exocarp (42/3) and the sister relationship with *Thevetia* suggest zoochory.

Colored fruits in the tribe are not restricted to leathery or fleshy mesocarps; within *Cerbera*, with spongy mesocarp (44/3), *C. manghas* L. has red exocarp (42/2), whereas *C. floribunda* K. Schum. and *C. odollam* Gaertn. have blue exocarp (42/0). The origin of a red exocarp is homoplastic (derived also in the *Thevetia* clade), which leads to the question of the

chemical nature of the color. Although this genus has colored exocarp, there are reports of water dispersal (Gunn & Dennis, 1976; Leeuwenberg, 1999), which can be correlated to the spongy texture of the mesocarp. In *Cameraria*, this condition can be interpreted as a result of an independent origin or as a common origin with respect to CCC. *Cameraria* and *Cerberiopsis* also share compressed fruits (40/1), but this condition is unambiguously optimized as having two independent origins. It has been suggested that the combination of spongy and flattened fruits allows them to be dispersed by wind or water (Veillon, 1971; Fallen, 1985). The sister relationship of *Cerbera* and *Cerberiopsis* would support the idea of hydrochory in *Cerberiopsis*.

The interpretation of seed dispersal mechanisms for *Allamanda*, which also has spongy mesocarp, is complicated given the wide diversity of morphologies of fruits and seeds among its species. In *A. cathartica* L., the spongy mesocarp is very thin, whereas in the CCC, it is well developed. Nevertheless, Fallen (1986) suggested hydrochory for this genus based on the spheroid shape of the fruit. The possible independent origin of the spongy mesocarp in combination with winged seeds (50/1) suggests that the dispersal mechanism for the genus is anemochory. Although the wings in the seeds of *A. cathartica* are heavy and contradict this idea, some species of *Allamanda* have papyraceous wings, which supports the hypothesis of wind dispersal. However, other species in the genus (e.g., *A. martii* Müll. Arg., *A. oenotheraefolia* Pohl., *A. puberula* A. DC.) have an exocarp with thorny projections, which could suggest zoochory (Mauseth, 1988).

CONCLUSIONS

The phylogenetic hypothesis for the tribe can be correlated to previous subtribal classifications, and the monophyly of subtribes Plumeriinae and Thevetiinae is supported by several synapomorphies. Allamandinae is accepted as a subtribe based on the sister position of *Allamanda* with respect to Thevetiinae. Nevertheless, this subtribe is taken as provisional due to conflict with molecular data.

Both *Cascabela* and *Thevetia* are supported as monophyletic so long as *T. pinifolia* is transferred to *Cascabela*. The combination and contrast of character states that support both clades (*Thevetia* and *Cascabela*) allow us to prefer the recognition of two generic entities instead of only *Thevetia* with two subgenera. *Cascabela* has five species, all of them present in Mexico and Central America except for two species endemic to Mexico. *Thevetia* has two species native to

South America and one growing from Mexico to South America. The sister group of the *Cascabela*–*Thevetia* clade remains uncertain, with two equally parsimonious possibilities: *Cerbera*–*Cerberiopsis* or *Anechites*–*Cameraria*. Similarly, the phylogenetic hypothesis of *Cascabela* at species level does not have hierarchical structure in the consensus. Therefore, the incorporation of a greater amount and type of information (morphological and molecular data and more species) is suggested. There is a need for continued research regarding macromorphology and micromorphology, which will allow us to propose new characters and re-evaluate the primary homology hypotheses. In the same way, it is necessary to invest in efforts to gather field observations and in experiments to improve our knowledge of reproductive and dispersal biology.

This cladistic analysis corroborates the relevance of the use of the morphology in phylogenetic reconstruction, recovering groups postulated by traditional taxonomy, as well as by molecular or combined phylogenies.

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APPENDIX 1. List of species. Numbering system applies to Appendices 1 and 2 only.

1. *Carissa macrocarpa* (Eckl.) A. DC.
2. *Allamanda cathartica* L.
3. *Anechites nerium* (Aubl.) Urb.
4. *Cameraria latifolia* L.
- 5a. *Cascabela gaumeri* (Hemsl.) Lippold
- 5b. *C. ovata* (Cav.) Lippold
- 5c. *C. pinifolia* (Standl. & Steyererm.) Alvarado-Cárdenas & Ochot.-Booth, comb. nov.
- 5d. *C. theretia* (L.) Lippold
- 5e. *C. theretioides* (Kunth) Lippold
- 6a. *Cerbera floribunda* K. Schum.
- 6b. *C. odollam* Gaertn.
- 6c. *C. manghas* L.
7. *Cerberiopsis candelabra* Vieill. ex Pancher & Sebert
8. *Himatanthus obovatus* (Müll. Arg.) Woodson
9. *Mortoniella pittieri* Woodson
- 10a. *Plumeria obtusa* L.
- 10b. *P. rubra* L.
- 11a. *Skytanthus acutus* Meyen
- 11b. *S. hancorniaefolius* (A. DC.) Miers
- 12a. *Theretia ahouai* (L.) A. DC.
- 12b. *T. amazonica* Ducke
- 12c. *T. bicornuta* Müll. Arg.

APPENDIX 2. Index to collections examined. Dagger (†) indicates specimens used in SEM analysis.

Acevedo, R. 249 (XAL) (2), 392 (MEXU) (5d), 953 (MEXU) (5b), 1029 (MEXU) (5b), 1298 (MEXU) (5b); Acosta 84 (MEXU) (5d); Acosta, S. 738 (MEXU) (5b), 806 (MEXU) (5b); Aguilar, C. 505 (MEXU) (12a), 806 (MEXU) (12a); Aguilar, G. 652 (MEXU) (12a), 1967 (MEXU) (12a); Aguilar, J. 55 (MEXU) (5b), 301 (MEXU) (5a); Aguilar, R. 230 (NY) (5b), 276 (MEXU) (5b), 287 (MEXU) (5b); Ahern's 21736 (NY) (6b); Alegria 79 (MEXU) (12a), Alexander 249 (NY)

(5b), 2163 (MEXU) (5c); Alexiades 1113 (NY) (5d); Almeda 287 (NY) (2); Alvarado 164 (NY) (5d); Alvarado-Cárdenas s.n. (MEXU†) (6b), 19 (MEXU†) (10b), 113 (MEXU†) (5b), 901 (MEXU) (5c) 901 bis (MEXU†) (2); Alvarado-Cárdenas et al. 20 (MEXU) (5c), 38 (MEXU) (5d); Alvarez, D. 63 (MEXU) (5a), 81 (MEXU) (12a), 424 (MEXU) (12a), 1210 (NY) (5a), 1509 (MEXU) (5a), 1624 (MEXU) (5a), 1734 (MEXU) (5a), 3894 (MEXU) (12a), 9126 (MEXU) (5a); Ambrosio, 289 (XAL) (2); Ankli 321 (MEXU) (5a); Annable 3380 (NY) (6b), 2864 (NY) (5d); Antonio, T. 1259 (NY) (12a); Aquino 98AA (MEXU) (5d), 170 (MEXU) (5b); Araquistain, M. 252 (MEXU) (5d), 2954 (MEXU) (5b), 3074 (MEXU) (5d), 3393 (MEXU) (12a); Argüelles 1055 (MEXU) (5c); Aristeguieta, L. 4690 (NY) (12a); Armstrong 1 (NY) (10b); Aronso, J. 7724 (MO) (11a); Atwood, J. & Nelly 46 (MEXU) (9); Ayora 45 (MEXU) (5a).

Bacab 103 (MEXU) (5a), 121 (MEXU) (5d), 159 (MEXU) (12a); Balam 13 (MEXU) (5a), 99 (MEXU) (5a), 421 (MEXU) (5a); Balanza 237 (Z) (7); Balcázar, T. 259 (MEXU) (12a); Balick, J. 1708 (NY) (12a); Balleza 7785 (MEXU) (5b), 8482 (MEXU) (5b), 8563 (MEXU) (5b); Bangham 636 (NY) (6b); Barajas 106 (MEXU) (5b); Barlow 29-10B (MEXU) (5d); Bartlett, H. 16436 (NY) (12a); Bates, D. 1685 (NY) (5d); Baumann-Bodenheim et al. 5097 (NY) (6b), 15297 (NY) (6b), 9779 (NY, Z) (7); Becerra s.n. (MEXU) (5b); Beck 1192 (NY) (6b), Beck, G. 2664 (MO) (12b); Bedel 2628 (MO) (3), Benítez 3107 (MEXU) (5b), 3137 (MEXU) (5b), 3806 (MEXU) (5b); Berlín s.n. (MEXU) (5c); Bernardi 482 (NY) (5d), 526 (NY) (5d), 20737 (NY) (5a); Bettie, A. 26128 (MO) (11a), 26129 (MO†) (11a), 26152-153 (MO) (11a); Billiet, F. & B. Jadin 5343 (MO) (11a); Black, G. & Ledoux, P. 50-10295 (MO, NY) (12b); Blanco 241 (XAL) (10b), 291 (XAL) (10b); Blanco, C. 971 (NY) (12a); Blum 983 (NY) (12a), 3987 (NY) (5d); Boege 99 (MEXU) (5c), 1912 (MEXU) (5d); Bojórquez 668 (MEXU) (5b); Bonpland 1341 (NY) (12a); Boom 6957 (NY) (5d), 10017 (NY) (5d); Boone 1205 (MEXU) (5b); Borden 24037 (NY) (6b); Boufford 25219 (NY) (6b); Brace 243-516 (NY) (5d); Breckon, J. 2045 (MEXU) (12a); Breedlove 28782 (MEXU) (12a), 34495 (NY) (12a), 51620 (MEXU) (5b); Brenes s.n. (NY) (5b), 17184 (NY) (5d), 22845 (NY) (5b); Brian 1239 (NY) (6c); Brigada Dioscóreas 2450 (MEXU) (12a); Brigada Vázquez 759 (MEXU, NY) (12a); Britton 1709 (NY) (5d); Britton 10025 (NY) (5d), 12954 (NY) (5d); Bruff 1107 (MEXU) (5b), 1278 (MEXU†) (5b); Brunner 1352 (MO) (12c); Buchholz, J. T. 1017 (NY) (6b); Bunting, G. 1277 (NY) (12a), 5033 (NY) (12a), 5110 (NY) (12a), 10215 (NY) (12a), 12767 (NY) (3), 12427 (NY) (12a), s.n. (NY) (12a); Bye, R. 15456 (MEXU) (12a).

Cabrera 24 (MEXU) (12a), 164 (MEXU, XAL) (2), 408 (MEXU) (5a), 445 (MEXU) (5a), 1098 (MEXU) (10a), 1171 (MEXU) (5a), 1262 (MEXU) (5a), 1273 (MEXU) (12a), 13505 (MEXU†) (12a), 2181 (MEXU) (5a), 2181 (NY) (5a), 2307 (MEXU) (12a), 2374 (MEXU) (10a), 2464 (NY, XAL) (4), 2485 (MEXU) (5a), 2475 (MEXU) (10a), 2581 (MEXU) (10a), 4667 (MEXU) (5a), 4789 (MEXU) (12a), 5933 (MEXU) (5b), 6327 (MEXU) (5a), 7223 (MEXU) (5a), 7381 (MEXU) (5b), 8036 (MEXU) (5d), 8919 (NY) (5d), 9041 (MEXU) (12a), 9640 (MEXU) (5a), 10250 (MEXU) (5a), 10747 (MEXU) (5a), 10747 (NY) (5a), 11328 (MEXU) (5d), 11696 (MEXU) (5a), 11793 (MEXU) (5a), 11798 (XAL) (4), 12592 (MEXU) (12a), 12661 (MEXU) (12a), 13494 (MEXU) (12a), 13505 (MEXU) (12a), 13622 (MEXU) (5d), 15412 (MEXU) (5a); Calderón Salvador 880 (NY) (5d); Callejas, R. 4915 (NY) (12a), 4936 (NY) (12a); Callejas, R. et al. 5010 (NY) (3); Calónico 3903 (MEXU) (5c), 4173 (MEXU) (5b), 5012 (MEXU) (5b), 8669 (MEXU) (5c), 15412 (MEXU) (5c), 23492 (MEXU) (12a), 23666 (MEXU) (12a), 23757 (MEXU) (12a), 23845 (MEXU) (10a), 23877

(MEXU) (5a), 24705 (MEXU) (12a); Calzada, J. 2375 (MEXU) (5d), 2666 (MEXU) (12a), 3861 (XAL) (10b), 4522 (MEXU) (5d), 5342 (XAL) (10b), 5644 (MEXU) (5d), 6326 (MEXU) (5d), 6335 (MEXU) (5d), 6422 (MEXU) (12a), 6586 (MEXU) (5a), 7819 (MEXU) (12a), 8429 (XAL) (10b), 9830 (MEXU) (12a), 10096 (XAL) (10b), 11169 (XAL) (2), 11516 (MEXU) (5d), 15016 (MEXU) (12a), 15430 (MEXU) (12a), 16071 (MEXU) (5b), 16713 (MEXU) (12a), 17690 (MEXU) (12a), 2375 (NY) (5d); Campos 133 (MEXU) (5d), 133 (MEXU) (5d), 2868 (MEXU) (5a), 2869 (MEXU) (5a); Campos-Villanueva 3722 (MEXU) (12a), 5162 (MEXU) (5b); Cancino 9 (MEXU) (5e); Cano 420 (MEXU) (5b); Carnevali, G. 5515 (MEXU) (12a); Carr 2217 (NY) (6b), s.n. (NY) (6b); Carranza 585 (MEXU) (5d); Carrasquilla 196 (MEXU) (12a); Carter 3163 (MEXU) (5d); Castañeda 41 (MEXU) (5c), 479 (MEXU) (5d); Castillo, G. s.n. (MEXU) (5d), 241 (XAL) (2), 406 (MEXU†) (12a), 2595 (MEXU) (5d), 3745 (MEXU) (12a), 5338 (XAL) (10b), 5864 (XAL) (10b), 6444 (XAL) (10b), 9311 (MEXU) (5b); Cayeros 226 (MEXU) (5e); Cedillo 21 (XAL) (2), 449 (MEXU, NY) (5b), 490 (NY) (5b), 728 (MEXU) (5b), 1006 (MEXU) (12a), 1385 (MEXU) (12a), 2872 (MEXU) (12a); Cedillo & Torres, R. 1445 (MEXU) (5e); Chan, C. 289 (XAL) (4), 536 (XAL) (2), 989 (MEXU) (5a), 1134 (XAL) (2), 1381 (MEXU) (5a), 3652 (MEXU) (12a), 3712 (MEXU) (12a); Chanek 33 (MEXU†) (5d); Charlotte 539 (NY) (5d); Chavelas ES4274 (MEXU) (12a), ES4216 (MEXU) (12a); Cházaro 1269 (MEXU) (5d), 3066 (XAL) (2), 3350 (XAL) (10b), 4836 (XAL) (10b); Chiang, F. 90 (MEXU) (5d), 536 (MEXU) (5b), 1021 (MEXU) (5b), 1021 (MEXU) (5b); Chiang, F. et al. F-1855 (MEXU) (5e); Chow 78136 (NY) (5d), 80206 (NY) (5d); Chrisophesen 656 (NY) (6b); Cibemiga 151 (NY) (5d); Clemens, J. 3384 (NY) (6b); Clemens, J. & M. Clemens s.n. (NY) (6c); College of Idaho s.n. (MEXU) (5b), M-935 (NY) (5e); Columbia College 1168 (NY) (11a); Conrad 2774 (MEXU) (12a); Conservator of Forest s.n. (NY) (10a); Constantino 7415 (NY) (6b); Contreras s.n. (MEXU) (5b); Contreras, E. 853 (MEXU) (5d), 8397 (MEXU†) (5a), 8397 (NY) (5a), 8483 (NY) (4); Conzatti 3951 (MEXU) (12a), 4631 (MEXU) (5e), 5278 (NY) (5e); Cooray 69073112R (NY) (5d); Correa, M. 10 (MEXU) (5a), 120 (MEXU) (5a), 260 (MEXU) (5a); Cortés 412 (MEXU) (5a), 473 (MEXU) (5a); Cortés, L. 310 (MEXU) (12a), 310 (MEXU) (12a), 392 (MEXU); Cowell 349 (NY) (12a); Crawford 566 (NY) (12a); Crawshaw, D. 284 (NY) (12b); Croat, T. s.n. (MEXU) (5d), 5032 (NY) (12a), 22561 (NY) (12a), 23527 (NY) (12a), 23561 (NY) (12a), 24907 (NY) (12a), 41864 (MEXU) (12a), 63241 (MEXU) (12a); Croat, T. & P. Duncan 16234 (MO) (3), 16361 (MO) (3); Cruz-Espinosa 899 (MEXU†) (10b); Curiel 192 (MEXU) (12a); Curran 3786 (NY) (6b); Curso de Ecología Vegetal p79 (MEXU) (12a).

Däniker 332 (Z) (7); D'Arcy, W. 16080 (MEXU) (12a); Darwin, S. 2347 (MEXU) (5a); Davidse, G. 9424 (NY) (12a); Degener 2451 (NY) (6b), 13718 (NY) (6b), 13768 (NY) (6b), 13978 (NY) (6b), 32077 (NY) (6b); Devia 845 (NY) (5d); Díaz, J. 5 (MEXU) (5d); Díaz, R. 132 (MEXU) (12a); Diego 7233 (MEXU) (5c), 7306 (MEXU) (5c); Dillon, M. & J. Teiller 5033 (MO†) (11a); Döbbeler 571 (MEXU) (5d); Dodson 5591-4261 (MO) (3); Dodson & A. Gentry 9792 (MO) (3); Donnell-Smith 2772 (NY) (5d); Dorado & Salinas F-2937 (MEXU) (5e); Dorantes s.n. (MEXU) (5d), 1001 (MEXU) (5d), 1264 (MEXU) (5d); Dressler 4292 (MEXU) (12a); Dreyer 337 (MEXU) (5a); Duery 61 (MEXU) (5b); Duke 9989(1) (NY) (3), 11398 (MO) (12b), 11398 (NY) (12b), 12209(2) (MO, NY) (3), 15445 (MO) (3); Duna 107 (NY) (12a); Duna, D. 23285 (NY) (5d); Durán R. 657 (MEXU) (10a), 948 (MEXU) (10a), 1518 (MEXU) (5a), 2833 (NY) (5a), 2853 (NY) (5a), 3502 (MEXU) (5a); Durán, A. 136 (MEXU) (12a); Durán, C. 285 (MEXU) (5d); Dwyer s.n. (MEXU) (5b).

Eames 4 (NY) (6b); Edaño 503 (NY) (6b); Egler, W. & H. Irving 45946 (NY) (12b); Ekman 15329 (NY) (3); Elmer 11997 (NY) (6b), 12173 (NY) (6b), 12896 (NY) (6b), 16773 (NY) (6b); Elmer, M. s.n. (NY) (6b), 1051 (NY) (6b); Elorsa s.n. (MEXU) (5b), 255 (MEXU, NY) (5b), 304 (MEXU) (5b), 3064 (MEXU) (5b), 3064 (NY) (5b), 4718 (MEXU) (5b), 5035 (MEXU) (5b); Enríquez, E. 44 (MEXU) (5b), 57 (MEXU) (5b), 924 (MEXU) (5b); Erlanson 5084 (NY) (6b); Escalante, S. 1 (MEXU) (5a), 885 (MEXU) (5a), 893 (MEXU) (12a); Escobar s.n. (MO) (3); Espejel, I. 604 (MEXU) (5a); Espinosa 1187 (MO) (3); Ewan 23023 (NY) (5d).

Fernández 3428 (NY) (5d); Fernández, A. 1333 (NY) (10b); Fernández, C. 10776 (NY) (5d); Ferrera 166 (NY) (10a); Figueroa 1 (MEXU) (5b); Figueroa, R. 53 (MEXU) (5b); Fisher s.n. (NY) (5d); Florence, J. 3931 (NY) (6b); Flores, A. 704 (MEXU) (12a); Flores, A. J. 1586 (XAL) (10b); Flores, J. 8313 (XAL) (4), 9711 (MEXU) (12a); Flores-Franco 1077 (MEXU) (5b), 2801 (MEXU) (5b), 3542 (MEXU) (5b), 3672 (MEXU) (5b), 5243 (MEXU) (5b); Fonnegra, R. 2808 (NY) (12a); Forero, E. 481 (MO) (3), 565 (MO) (3), 1590 (NY) (12a); Fosberg, R. 9375 (NY) (5d), 25397 (NY) (5d), 50992 (NY) (6c), 56596 (NY) (6c); Foxworthy 42135 (NY) (6b); Fragoso, R. s.n. (MEXU) (5b), s.n. (MEXU) (5b); Franc, I. 545 (NY) (7); Franco 52 (MEXU) (5b); Freeland, J. 139 (MEXU) (5d); Frei FRE1019 (MEXU) (5d); Frodin, D. 26615 (NY) (6b); Froes 30535 (MEXU) (12b); Frye 2586 (NY) (5e); Fryxell 3543 (NY) (5d); Fuchs 1697 (MEXU) (5d); Fuentes s.n. (MEXU) (5a), s.n. (XAL) (10b).

Gallardo, C. 609 (MEXU) (5b), 2226 (MEXU) (5a); Garber 959 (NY) (5d); García-Mendoza 646 (MEXU) (5b), 3221 (MEXU) (5d), 4097 (MEXU) (5b); García-Mendoza et al. 297 (MEXU) (5c); Gaumer 546 (NY) (5d), 22110 (MEXU) (12a); Genelle 899 (NY) (5e); Gentle 336 (NY) (5a), 4751 (NY) (5a); Gentry, A. 8071 (NY) (12a), 8198 (NY) (12a), 8484 (NY) (12a), 22757 (NY) (5d), 26296 (MO) (3); Gentry, A. & Dodson, C. 35722 (MO) (3), 41299 (MO) (3); Gentry et al. 43913 (MEXU†) (9); Gentry, H. 5028 (MEXU, NY) (5b), 5157 (MEXU, NY) (5b), 10929 (MEXU) (5b); Gereau R. E. 2204 (MEXU) (12a); Germán 479 (MEXU) (5b); Gilly 1 (NY) (5e), 51 (NY) (5d); Glassman 1819 (NY) (5b); Godínez 4 (MEXU) (5e); Gómez s.n. (MEXU) (5b); Gómez-Pompa 88 (MEXU) (12a), 107 (MEXU) (12a); Góngora 650 (MEXU) (12a); Gonzales, A. 209 (NY) (5d); González, E. 692 (MEXU) (5d); González, R. 282 (MEXU) (5c); González, S. 2403 (MEXU) (5b); González-Medrano 5068 (MEXU) (5b); González-Medrano et al. F-613 (MEXU) (5e); Goreti 633 (MEXU) (5c); Granville 9604 (NY) (2), 10285 (NY) (2); Greenwood R1913 (NY) (12a); Gregory s.n. (MEXU) (5b), 324 (NY) (5b); Grether 1727 (MEXU) (5b); Guadarrama 885 (NY) (12a), 6568 (MEXU) (12a); Guaglianone et al. 468 (NY) (12c); Guerrero, B. 305 (XAL) (2), 1782 (XAL) (10b); Guerrero, S. 328 (XAL) (10b); Guillaumin, A. et al. 13181 (NY) (7); Guillen & Coria 1584 (MO†, NY) (12b); Gillespie, J. 2071 (NY) (6b), 2267 (NY) (6b), 3643 (NY) (6b), 3731 (NY) (6b); Guizar, E. 80 (MEXU) (5b), 2869 (MEXU) (5b); Gutiérrez, C. 1838 (MEXU) (5d), 4635 (XAL) (4), 5691 (NY) (4); Gutiérrez, L. 174 (MEXU†) (12a); Gutiérrez, R. 240 (MEXU) (5a); Guzmán 477 (XAL) (10b), 901 (XAL) (10b); Guzmán, M. 344 (MEXU) (5d), 411 (MEXU) (5b).

Hagen 1374 (NY) (12a); Halsted s.n. (NY) (5d); Hammel, B. & W. D'Arcy 5028 (MO) (3); Hansen, B. 1518 (MEXU) (5b), 7518 (NY) (5d), 7557 (NY) (5d); Harley et al. 26444 (NY†) (11b); Hatschbach 29551 (NY) (12c), 47443 (NY) (11b), 52491 (NY) (12c), 52730 (MEXU) (8); Hasskahl s.n. (NY) (6c); Hassler 7453 (MO, NY) (12c); Hayes, S. 277 (NY) (5d); Henry, A. 12747 (NY) (5d); Henty, E. 27211 (NY) (6b); Herb. Mus. Nat. Vindobon 5159 (NY) (5d); Heringer et al.

845 (NY) (12c); Hernández, A. C. 70 (NY) (5d), 3922 (MEXU) (5d), 9420 (MEXU) (5b); Hernández, A. D. s.n. (XAL) (10b); Hernández R. 19 (XAL) (2); Hernández del Olmo 618 (MEXU) (12a); Herrera, A. 128 (MEXU) (5d); Hesse, A. 1072 (NY) (6b); Heyden 3995 (NY) (5d); Hinton, G. s.n. (MEXU) (5b), 3792 (NY) (5c), 5716 (NY) (5c), 5732 (NY) (5c), 7579 (MEXU†) (5c), 7579 (NY) (5c), 7961 (NY) (5c), 9178 (NY) (5c), 10532 (NY) (5c), 11153 (NY) (5c), 12018 (MEXU) (5c), 12018 (NY) (5c); Hitchcock, A. 16864 (NY) (2); Hohenacker, R. 45 (NY) (6c); Holdridge 102 (NY) (5d); Hosokawa, T. 9670 (Z) (6a); Howard, R. 4179 (NY) (5d), 9301 (NY) (5d), 19088 (NY) (5d); Huft, M. et al. 1963 (MO) (3); Hughes 1940 (MEXU) (5b), 1940 (MEXU) (5b); Humbert H. 26511 (NY) (5d); Hunt 5450 (NY) (5d); Hunter, A. 437 (NY) (12a); Hurlimann H. 13 (NY) (6b), 24 (NY) (6b), 342 (NY†) (7), 624 (NY) (6b); Hutchison, C. 3123 (NY) (5d).

Ibarra 320 (MEXU) (5b).

Jack 8366 (NY) (12a); Jeffrey 688 (NY) (6b); Jenman 48-2 (NY) (5d); Jiménez, 4962 (NY) (3); Jiménez, Q. 11651 (NY) (5b); Jones 3101 (NY) (12a), 3425 (MEXU) (12a), 3425 (NY) (12a); Jorgenow 2065 (MO) (12c).

Kanchira 121 (NY) (6b), 468 (NY) (6b), 470 (NY) (6a), 1936 (NY) (6a), 2279 (NY) (6a); Kennedy 2834 (MO) (3); Kiesling 9702 (MEXU) (12c); Killeen 6997 (MEXU†) (12b); Killip s.n. (NY) (5d); King 1652 (NY) (5b); Klug 4006 (NY) (5d); Knapp 1906 (NY) (12a); Knapp & Mallet 3905 (MO) (3); Kocyan 991017 (MEXU†) (6c); Krapovickas & Cristobal 44169 (NY) (12c); Krug 7179 (SP) (5d); Krukoff 6297 (NY) (5d); Kuntze s.n. (NY) (5c), 16 (NY) (5d); Kuswata 6 (NY) (6b).

Ladd 264 (MEXU) (5c); Lammers et al. 7621 (MO, NY) (11a); Langlassé 269 (MEXU) (5b); Langman 3325 (MEXU) (5c); Lansing 2025 (NY) (5d); Lau 313 (NY) (6b); Laughlin 2667 (MEXU) (5b); Laughman 3325 (MEXU) (5d), 3325 (MEXU) (5d); Leavenworth 207 (NY) (5d); Lee 2107 (NY) (6b); Leeuwenberg s.n. (NY) (6c); Lei 787 (NY) (5d); Leonard 3640 (NY) (5d); Lewis 59 (MEXU) (12a); Lienser 3864 (NY) (5d); Limón s.n. (MEXU) (5b); Linares 3315 (MEXU) (5d), 5343 (MEXU) (5b); Liogier 26850 (NY) (3), 36134 (NY) (4); Lira 800 (MEXU) (10a), 916 (MEXU) (5a), 1045 (MEXU) (5a), 1051 (MEXU) (5a); Littmann E. 9042 (NY) (10b); Lomelí, J. A. 3367 (MEXU) (5c); López H. E. 266 (MEXU) (12a); López, M. 19 (NY) (5d); López, M. G. 109 (MEXU†) (12c); López, W. 1128 (MEXU) (5c), 1193 (MEXU) (5d); Lorea 5100 (MEXU) (5d); Lorence 3513 (MEXU) (12a), 5034 (MEXU) (1); Lorence et al. 3777 (MEXU) (5c); Lott 430 (MEXU) (5b), 1223 (MEXU) (5b), 2089 (MEXU) (5b); Lozada 74 (MEXU) (5b); Lundell 984 (NY) (5a), 1011 (NY) (12a), 1047 (MEXU) (12a); Lyonnet 550400017 (MEXU) (5b).

MacDougal 643s (NY) (12a); Machuca 639 (XAL) (10b); Madrid 105 (MEXU) (12a), 878 (MEXU) (5a), 1059 (MEXU) (5a); Magallanes 715 (MEXU) (5b), 4651 (XAL) (10b); Magaña 299 (MEXU) (12a), 478 (XAL) (2); Manzanero 1015 (MEXU) (5b), 1111 (MEXU) (5b); Mariz 489 (SP) (5d); Márquez 871 (MEXU) (5d); Marshall 6669 (NY) (5d); Martínez C. 21 (XAL) (2), 2129 (MEXU) (5b), 771 (MEXU) (5b), 2129 (MEXU) (5b); Martínez, E. 295 (NY) (5c), 1336 (MEXU) (5c), 1336 (NY) (5c), 2008 (MEXU) (12a), 3639 (MEXU†) (5c), 4588 (MEXU) (5b), 6324 (MEXU) (5d), 7162 (MEXU) (12a), 13599 (MEXU) (12a), 20343 (MEXU) (5b), 20928 (MEXU) (12a), 27042 (NY) (4), 27067 (MEXU) (5a), 27107 (MEXU) (5a), 27540 (MEXU) (5a), 30371 (MEXU) (5a), 35944 (MEXU) (5a); Martínez, E. et al. 2001 (MEXU) (5c), 35058 (MEXU) (12a); Mata 87-103 (MEXU) (5d); Matsuo 44 (NY) (6b); Matuda 3078 (MEXU) (12a), 4659 (MEXU) (5b), 31264 (MEXU) (5b); May 917 (MEXU) (12a), 904 (MEXU) (12a); Maya 1704 (NY) (10b); McPherson 3367

(MO†, Z) (7), 3823 (MO) (7), 3823 (MO) (7); Meagher 939 (MEXU†) (3); Medina 427 (MEXU) (5d); Medina, R. s.n. (MEXU†) (1); Mejía, S. M. T. 1615 (MEXU) (5d); Méndez, D. 76 (MEXU) (5a); Méndez, F. 296 (XAL) (4); Méndez, M. 943 (MEXU) (5a), 694 (MEXU) (5a); Méndez, T. 5894 (XAL) (10b); Mercedes 3550 (MO) (12c); Merrill 3804 (NY) (5d); Meyen 4394 (MO) (11a); Mille 60 (NY) (5d); Miller 101 (NY) (5d); Miranda, A. 950 (MEXU) (5b); Miranda, F. 39 (MEXU) (5c), 424 (MEXU) (5b), 1509 (MEXU) (5b), 4229 (MEXU) (12a), 8075 (MEXU) (5a); Molina 224 (MEXU) (5b), 11008 (NY) (5b), 15633 (NY) (12a), 22437 (NY) (5b), 34933 (MEXU) (5b); Monroy de la Rosa 313 (MEXU) (5b); Montalvo 6376 (NY) (5b); Moraes et al. 1465 (NY) (12b); Morales 2929 (MEXU) (5b), 5028 (NY) (5b), 5726 (NY) (5b); Morales, M. 51 (XAL) (2); Moreno 776 (MEXU) (5b), 1237 (MEXU) (5b), 3629 (MEXU) (5b), 5476 (MEXU) (5b), 6845 (MEXU) (5d), 8551 (MEXU) (5d), 22181 (MO) (3), 24496 (MEXU†) (9), 24625 (MEXU) (12a), 24886 (MEXU) (9); Moreno P. 670 (MEXU) (10a), 2450 (MEXU) (5b), 6502 (MEXU) (5b), 8223 (MEXU) (5b), 139 (MEXU, NY) (5a); Mori 22132 (NY) (2); Moritz 1158 (NY) (12a); Morong 381 (MO) (12c), 642 (NY) (5d), 1168 (MO) (11a); Mostacedo, B. et al. 2641 (MEXU†) (8); Müller 1853 (NY) (5d); Muñoz et al. 2790 (MO) (11a); Murca 1797 (MO) (12b); Murillo 329 (NY) (10b).

Narváez 225 (MEXU) (5a); Nash 601 (NY) (3); Nee 18464 (MEXU) (5d), 26649 (XAL) (10b), 27085 (XAL) (2), 28273 (NY) (5b), 28477 (MEXU) (5d), 28477 (NY) (5d), 29341 (NY) (2), 29341 (XAL) (2), 35194 (NY) (5d), 37194 (NY) (12b), 41121 (NY) (5d); Neill 2572 (MEXU) (12a); Nervers 8303 (MEXU) (12a); Nevling 468 (MEXU) (5d); Niyomdham 1649 (NY) (6c); Noriega 22 (MEXU) (5c).

Ocaña 160 (MEXU) (12a); Ochoterena 271 (MEXU†) (5c); Oliveira 52 (SP) (5d); Orellana 289 (MEXU) (12a); Ortega, L. 117 (XAL†) (2), 431 (XAL) (2); Ortiz, G. 327 (MEXU) (5b); Ortiz, J. 331 (MEXU) (5a).

Palacios s.n. (MEXU) (5c); Palma s.n. (MEXU) (12a); Palmer, E. 27 (MEXU, NY) (5c), 339 (NY) (5d), 1069 (NY) (5b), 1533 (NY) (5b); Pancher s.n. (MO, NY) (7); Paniagua 610 (MEXU) (12a); Pascual 491 (MEXU) (5d); Peck 807 (NY) (12a); Pennell 4234 (NY) (12a), 9211 (NY) (5b); Peña-Chocarro 571 (MEXU) (5a); Peralta 378 (MEXU) (5c); Pere 2611 (NY) (5d); Pérez, A. 248 (MEXU) (5b), 861 (MEXU, NY) (5b); Peterson 2 (NY) (6c); Pfeifer 1677 (MEXU) (5b); Pipoly 4875 (MO) (3); Pittier 12099 (NY) (12a), 13071 (NY) (3); Plowman 13763 (NY) (10b); Poilane 1351 (NY) (5d); Pringle 4107 (NY) (5d), 6332 (MEXU, NY) (5b), 6739 (NY) (5b); Prinzie 157 (MEXU) (5b); Pueh 373 (MEXU) (5a); Puga 17003 (MEXU) (5b); Puig 4646 (MEXU) (5d); Pulido s.n. (MEXU†) (5a); Purpus 3235 (NY) (5c).

Quero 2424 (MEXU) (5a), 2758 (MEXU) (12a); Quezada 1699 (MEXU) (5b); Quipuscoa 797 (NY) (5d).

Ramamoorthy 2692 (MEXU) (12a), 2067 (MEXU) (5a), 2448 (MEXU) (12a), 4307 (MEXU†) (5c); Ramírez s.n. (MEXU) (5c), s.n. (MEXU) (5c); Ramos 363 (MEXU) (12a); Ratter et al. 5941 (NY) (12c); Renson 232 (NY) (5d); Reyes-García 48 (MEXU) (5b), 761 (MEXU) (5b), 802 (MEXU) (5b), 1118 (MEXU) (5b), 1955 (MEXU) (5b), 2022 (MEXU) (12a), 2370 (MEXU) (12a), 2866 (MEXU) (5b), 5362 (MEXU†) (5b); Ribera 717 (MEXU) (5b); Rico-Gray 472 (XAL) (4); Rimachi 5784 (NY) (5d); Rimcahi 10217 (NY) (5d); Rincón 1011 (MEXU) (12a), 1613 (MEXU) (12a), 1672 (MEXU) (12a); Rinehart A. LR23351 (NY†) (6a); Ritter 4592 (MO) (12c); Rivera 2 (NY) (5d); Rivera, J. 717 (NY) (5b), 780 (NY) (5b); Robles 681 (XAL) (10b), 893 (MEXU) (12a); Robleto 775 (MO) (3), 986 (MO) (3), 1007 (MEXU) (5a), 1202 (MO) (3), 1329 (MO) (3); Rodríguez, D. 6 (NY) (5b); Rodríguez, G. s.n. (NY) (2); Romero 497 (XAL) (10b); Romero-Castañeda

6324 (MO†) (3), 9743 (NY) (5d), 6324 (NY) (3); Rosas 618 (MEXU) (5d); Rubio 2403 (MEXU) (5d); Ruenes, R. 73 (MEXU) (1); Rusby 361 (NY) (5d); Rzedowski 12233 (MEXU) (5e), 22307 (MEXU) (5e), 34203 (MEXU) (5b), 35724 (MEXU) (5e), 39849 (MEXU) (5e).

S.c. s.n. (NY†) (11a); Salas 2102 (MEXU) (5b); Saldias 570 (MO, NY) (12b); Saldivar 28 (MEXU) (5b); Salinas, F. 3856 (XAL) (10b), 4266 (XAL) (10b); Salinas & Solis-Sánchez F-3497 (MEXU) (5e); Salsedo 157 (NY) (6b); Sandino 655 (MEXU) (5d); Santana 2956 (MEXU) (5b); Santiago 617 (MEXU) (5b); Sauders 1032 (NY) (2), 1042 (NY) (2); Saynes 2674 (MEXU) (5b); Schmitz 748 (NY) (5e); Schubert 1688 (MEXU) (5a); Scolnik & Luti 671 (NY) (12b); Seibert 385 (NY) (12a); Seigler 13583 (NY) (5e); Shunsuke, B. 1241 (NY) (2); Silva 6237 (SP) (5d); Simá 1249 (MEXU) (5a), 1668 (MEXU) (5a); Sinaca, M. 2040 (MEXU) (12a); Sintenis 1650 (NY) (5d); Small 638 (NY) (5d), 8855 (NY) (5d); Smith 68 (NY) (6b), 1581 (NY) (6b), 1661 (MO, NY) (3), 1839 (NY) (6b), 4708 (NY) (6b), 5276 (NY) (6b), 5801 (NY) (6b), 7913 (NY) (6b), 8524 (NY) (6b), 8897 (NY) (6b), 9201 (NY) (6b); Soejarto 5997 (NY) (6b); Sohmer 9381 (MEXU) (5d); Sol 812 (MEXU) (12a); Solheim 1763 (MEXU, NY) (5d); Solís-Magallanes 3033 (MEXU) (5b); Sorensen 7074 (XAL) (4); Soto, J. 660 (MEXU) (5c), 1151 (MEXU) (5c), 2038 (MEXU) (5c), 3339 (MEXU) (5b), 4274 (MEXU) (5e), 4277 (MEXU) (5c); Sousa 8544 (MEXU) (1), 10961 (MEXU) (5a); Standley, P. 21615 (NY) (5b), 20839 (NY) (5b), 22012 (NY) (5d); Stevens 3663 (MEXU) (9), 22296 (MEXU†) (9), 24126 (MEXU) (12a); Steyermark 50708 (NY) (5b); Struwe 1216 (NY) (6b).

Tahir 699 (NY) (6c); Tapia s.n. (MEXU) (5a); Tapia & Carnevali 1386 (MEXU) (10a); Taylor 4403 (NY) (5b); Taylor, C. 10795 (MO) (11a); Teiller 878 (MO) (11a); Téllez 5610 (XAL) (4), 5621 (XAL) (4), 9959 (MEXU) (5b), 10472 (MEXU) (5b), 2175 (MEXU) (12a); Tenorio 14579 (MEXU) (12a), 19507 (MEXU) (5d); Tenorio & Alvarado-Cárdenas 20638 (MEXU) (5e); Tenorio & Kelly 21685 (MEXU) (5e); Tenorio et al. 21617 (MEXU) (5e); Tessmann, G. 3237 (NY) (5d); Thomas, W. et al. 4559 (MO, NY) (12b); Tiwari 349 (NY) (2); Toledo 291 (NY) (5c); Toro 451 (NY) (5c); Torres, L. 154 (MEXU) (5b); Torres, R. 6462 (XAL) (2), 11849 (XAL) (10b); Torres, R. & Tenorio 12797 (MEXU) (5e); Tovar R. C. 133b (XAL) (2), 216 (XAL) (2); Trott S. s.n. (NY) (5e); Tsui 212 (NY) (6b); Tún 1076 (NY) (10b).

Ucán 992 (XAL) (4), 3606 (MEXU) (5a).

Valle s.n. (MEXU) (5d); Vanpel 399 (NY) (6b); Vázquez 864 (XAL) (10b); Vega, A. 2802 (MEXU) (1); Ventura, F. 1239 (MEXU) (5e), 17876 (MEXU) (12a); Ventura, E.-López, E. 281 (XAL) (2), 1555 (XAL) (2), 1003 (XAL) (10b), 3611 (XAL) (10b), 21241 (NY) (12a); Villanueva 805 (XAL†) (4); Villareal 6755 (MEXU) (5b); Vink 12190 (Z) (6a).

Walther 340 (NY) (5d); Wang, Y. 3190 (NY) (6b); Wang, C. 34989 (NY) (6b); Waterhouse 226 (NY) (6b); Weber 1133 (NY) (6b); Wedel 2570 (MO) (3); Werdermann 136 (MO) (11a), 2597 (MO) (12c); White, D. 224 (MEXU, NY) (5a); Whitford 700 (NY) (6b); William, R. 2853 (NY) (6b); Williams 22455 (NY) (5b); Wilson 317 (NY) (5d), 1072 (NY) (11b), 2221 (NY) (11b); Woodson 1524 bis (NY) (12a); Worth, C. & J. Morrison 16162 (MO) (11a); Worthington 12398 (NY) (6c); Wright 1663 (MO) (3); Wurdak 300 (NY) (2).

Yuncker 4967 (NY) (10b), 6091 (NY) (2), 8284 (NY) (12a), 9134 (NY) (6b), 15106 (NY) (6b), 15730 (NY) (6b), 15867 (NY) (6b), 18325 (NY) (5d).

Zarucchi 3260 (NY) (5d), 4923 (NY) (5e); Zizumbo 151 (XAL) (10b), 1152 (XAL) (10b), 1153 (XAL) (10b); Zöllner 11373 (MO) (11a).

APPENDIX 3. Morphological characters and character states.

(0) Life form: 0 = vine; 1 = shrub; 2 = tree. This character was used by Endress et al. (1996), coding as the same character state trees and shrubs, considering the fact that both, in contrast to perennial herbs, have secondary growth and do not die in the winter. Here, we consider that trees and shrubs can be recognized as two distinct states; in natural conditions, trees are woody plants with a main axis that branches above ground, whereas in shrubs, it is not possible to distinguish a main axis because the plant branches from the base (Lawrence, 1958; Radford, 1986; Sousa & Zárate, 1988; Alvarado-Cárdenas & Ochoterena, pers. obs.). Given that some authors consider the difference between these two life forms merely by measuring the height of the plants, this feature was coded only from personal observations or from descriptions that allowed us to clearly define both states by means of the ramification pattern. The vines were used by Endress et al. (1996) as a different state, a coding with which we agree because vines generally have different physiological and biomechanical adaptations.

(1) Phyllotaxis: 0 = alternate; 1 = opposite; 2 = verticillate (additive). Phyllotaxis has been an important character in taxonomic and phylogenetic Apocynaceae works. Sennblad et al. (1998) regarded the verticillate condition as a variation of opposite leaves, because in the plants with verticillate leaves there are also opposite ones. Furthermore, they did not consider verticillate phyllotaxis as a character state because in their sampling, it would have represented an autopomorphic condition of *Nerium oleander* L. In contrast, Endress et al. (1996) considered verticillate leaves as a distinct character state, even though they pointed out that in the taxa with this phyllotaxis it is also possible to find opposite or alternate leaves, but they only grow just below the inflorescences. We take the position of Endress et al. (1996), coding the character states from leaves that are not subtending inflorescences, not only because we consider that the three states represent valid homology hypotheses, but also because the verticillate condition distinguishes *Allamanda* from the remaining genera, representing a potential synapomorphy for the genus. This character was here considered as additive because it represents a logical transitional series of decrease in internodal distances.

(2) Leaf blade shape: 0 = lanceolate; 1 = ovate; 2 = obovate. Liede (1994) coded for some subtribes within Asclepiadoideae two states for this character: “0 = non-linear, 1 = linear.” She considered that the variation in shape within the sampled taxa was restricted to linear vs. ovate-obovate (coded as nonlinear). Nevertheless, the recognition of just two character states could hide potential homologies among ovate and obovate leaves. Bruyns and Linder (1991) proposed the states “0 = lorate, 1 = deltoid” for some genera of Asclepiadoideae. Here we recognize a more comprehensive range of variation that applies to Plumerieae, coding the states according to the patterns suggested by Radford (1986).

(3) Presence of indumentum on vegetative parts: 0 = no; 1 = yes. This character and its states follow the proposal of Williams (2002).

(4) Secondary veins: 0 = exposed; 1 = immersed. The character and its states follow the proposal of Williams (2002).

(5) Presence of branching in the inflorescence: 0 = no; 1 = yes. This character has never before been incorporated into phylogenetic analyses. Among the sampled taxa, some species have inflorescences that never branch,

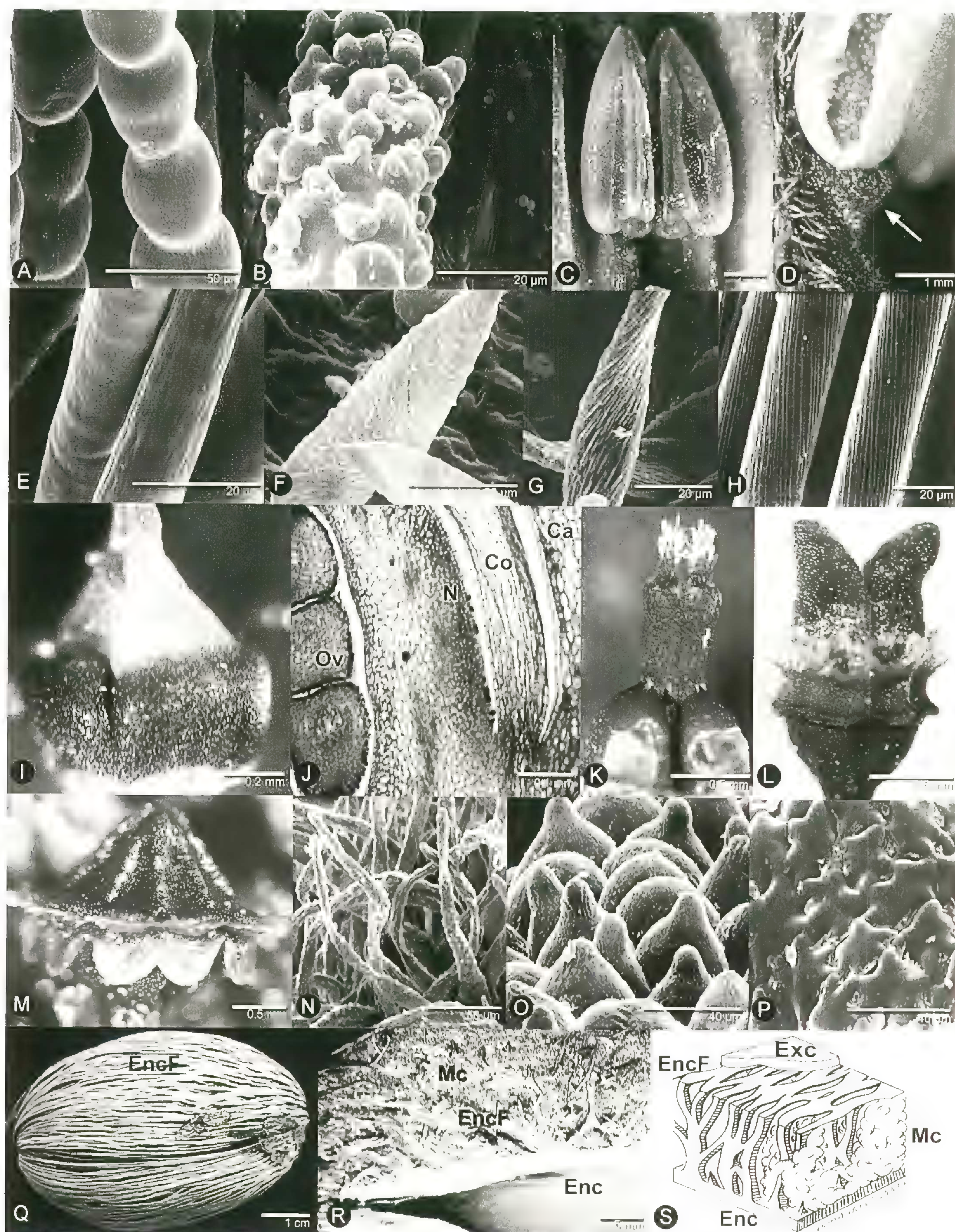


Figure 4. Selected characters and character states used in the phylogenetic analysis. A, B. Absence/presence of ornamentation of the supracolumnar trichomes (character 15). —A. Not ornamented (*Allamanda cathartica* [Alvarado-Cárdenas 901 bis]). —B. Ornamented (*Plumeria rubra* [Alvarado-Cárdenas 19]). C, D. Structures related to the anthers' support (character 17). —C. Filament (*Himatanthus obovatus* [Mostacedo, B. et al. 2641]). —D. Rib (arrow) (*Cerberiopsis candelabra* [McPherson 3367]). E, H. Absence/presence and pattern of ornamentation of the infrastaminal trichomes (characters 29 and 30). —E. Absence (*Allamanda cathartica* [Alvarado-Cárdenas 901 bis]). —F. Verrucose (*Anechites nerium* [Romero-Castañeda 6324]). —G. Discontinuous striations (*Theretia amazonica* [Guillen & Coria 1584]). —H. Continuous striations (*Cascabela gaumeri* [Pulido s. n.]). I, J. Presence of nectary on the ovary (character 31, state 1). —I. General aspect of the nectary (*Cameraria latifolia* [Meagher 939]). —J. Longitudinal section of the flower. Ca = Calyx, Co = Corolla, N = Nectary, and Ov

whereas others produce more than one reproductive axis subtended by a single leaf.

(6) Presence of a dominant axis in inflorescences that branch: 0 = no; 1 = yes. Among the inflorescences that branch, two patterns can be distinguished. In some cases, the inflorescences develop a main axis (sympodial growth), whereas in others, the branching axes reach the same or more or less the same size and, hence, it is not possible to recognize a main axis. Species without branching inflorescences were coded as inapplicable (-).

(7) Length of the bracts subtending the flowers (mm): 0 = 0.5–4.0; 1 = 4.0–11.5; 2 = 11.5–20.0 (additive). This character has been used in taxonomic works, but not in phylogenetic analyses. Here we defined and coded the character states according to the results of descriptive statistics (see “Material and Methods”). Furthermore, the states were coded as additive because they can imply a logic transitional series of increase or decrease.

(8) Sepal form: 0 = ovate; 1 = obovate. The character states are defined according to Radford (1986). Our observations showed that sepal form is constant at species level and that both character states are unambiguously assignable.

(9) Sepal length (mm): 0 = 0.5–4.0; 1 = 4.0–11.0; 2 = 11.0–20.0 (additive). Williams (2002) coded this character for species in tribe Echiteae, recognizing the states: “0 = minute (0–3 mm), 1 = foliaceous (5–15 mm).” Within Plumerieae, we suggest an adjustment of those intervals according to descriptive statistics. At the same time, the measurements were modified starting from 0.5 mm instead of zero because to suggest a sepal length of 0 mm could be interpreted as absence of the structure, which is never the case. This character was coded as additive because there is a potential transitional series of increase or decrease.

(10) Presence of glands at the tip of the sepals: 0 = no; 1 = yes. In Apocynaceae, the existence of glands at the tip of the sepals is a rare condition, occurring in only a few genera, among which are *Anechites* (Fallen, 1983) and *Plumeria* (Woodson, 1938a). This character has not been used before in cladistic analyses, but its presence in the same position and in species of the same tribe allows us to postulate it as a potential homologous condition.

(11) Presence of colleters on calyx: 0 = no; 1 = yes. Colleters are important structures generally employed in taxonomic treatments and phylogenetic studies. Endress et al. (1996) considered the variation in sepal colleter number to recognize three conditions within this character: “0 = absent, 1 = 20–50, 2 = 5.” Instead, Williams (2002) considered their position and number, recognizing the following states: “0 = absent, 1 = numerous and alternate to the sepals, 2 = solitary and opposite to the sepals.” Both proposals cannot be applied to species in Plumerieae because the number of colleters is very variable among individuals from the same species (e.g., from absent to 65). On the other hand, when colleters are present in members of

this tribe, they are always opposite to the sepals. Therefore, in this study we only consider absence or presence.

(12) Corolla shape: 0 = hypocrateriform (Fig. 1E); 1 = funnelform-tubular; 2 = funnelform-campanular (Fig. 1C, D). The different shapes of the corolla follow the proposals of Font Quer (1982), Radford (1986), and Sousa and Zárate (1988). The corolla of *Thevetia amazonica* Ducke has been considered as funnelform (Gensel, 1969), but here it is coded as hypocrateriform, because the throat expands only at the staminal region, but it recovers its diameter outside this region, as it occurs in other flowers considered as hypocrateriform (e.g., *Catharanthus roseus* (L.) G. Don or *T. ahouai* (L.) A. DC.).

(13) Presence of supracorollary appendages: 0 = no; 1 = yes. The term “supracorollary appendages” was coined by Pichon (1948a) and used by Gensel (1969), referring to the structure that sometimes develops above the anthers. The term “corolline corolla,” used by Endress et al. (1996), corresponds to this same condition. These structures have taxonomic and phylogenetic importance. Williams (2002) suggested three states: “0 = absent, 1 = reduced to a callous ridge, 2 = extended into a staminode,” but only the first and third apply to our sampling. Therefore, we are coding absent/present as Endress et al. (1996).

(14) Supracorollary appendages shape (Fig. 3): 0 = deltoid; 1 = oblanceolate; 2 = digitiform. The shape of these structures was somehow considered by Williams (2002; see previous character), but he combined in his states a mixture of qualities: shape, size, and texture. Here, we adjust the shapes according to personal observations and following Radford (1986).

(15) Presence of ornamentation on the supracorollary trichomes: 0 = no (Fig. 4A); 1 = yes (Fig. 4B). The ornamentation on the supracorollary trichomes has been reported within the tribe for species of *Himatanthus* and *Plumeria* (Pichon, 1948b), but was never before employed in cladistic analyses. Our personal observations show that these ornamentations are present in other taxa not previously reported (Table 3) and that their absence or presence is constant within species.

(16) Presence of a structure supporting the anther: 0 = no; 1 = yes. The anthers in Plumerieae can be sessile or supported by a filament or a projection of the corolla called rib (Fallen, 1986; Williams, 2002). Williams coded two characters related to the structures of support. One was the presence of a filament, considered to be one of three states: “0 = minute (0–1 mm), 1 = medium (3–6 mm), 2 = long (10 mm or more);” the other was the presence of ribs, coding them as absent/present. However, both structures (filaments and ribs) occupy the same position and apparently have the same function, and, therefore, we considered filaments and ribs as alternative homologous conditions (next character). On the other hand, a length of 0 mm could be interpreted as sessile anthers, and at the same time in our

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= Ovule. K–M. Relative position of the stigmata (characters 35, 36, 38). —K, L. Not convergent (*K. Mortoniella pittieri* [Moreno 21196]; *L. Skytanthus acutus* [s. coll. s.n.]). —M. Convergent (*Cascabela gaumeri* [Pulido s.n.]). N–P. Shape of the stigmata cells (character 37). —N. Filiform (*Carissa macrocarpa* [Medina s.n.]). —O. Conic (*Cerbera manghas* [Alvarado-Cárdenas s.n.]). —P. Irregularly flattened (*Plumeria rubra* [Alvarado-Cárdenas 19]). Q–S. Fruit layers of *Cerbera* (characters 44/3, 45/2, 46/1, 47/1). —Q. General aspect of the fruit after removing the exocarp (*Cerbera odollam* [Rinehart A. LR23351]). —R. Longitudinal section of the fruit after removing the exocarp showing the endocarp with the fibers extending toward the spongy mesocarp (*Cerbera odollam* [Rinehart A. LR23351]). —S. Schematic section of the fruit showing all layers. Enc = Endocarp, EncF = Endocarp fibers, Mc = Mesocarp, Exc = Exocarp.

sampling ribs measure more than 1 mm, so the rank for the states is here adjusted.

(17) Shape of the structure supporting the anther: **0** = **filamentous** (Fig. 4C); **1** = **rib** (Fig. 4D). In the absence of ontogenetic or anatomical studies, we consider that the filaments and the ribs have an equivalent function and position. Thus, we postulate that both states, cylindrical and not rigid vs. flattened and rigid restricting the movement of the anthers, represent alternative homologous conditions.

(18) Anther dehiscence position: **0** = **introrse** (Fig. 4C); **1** = **latrorse** (Fig. 4D). The character and its states are taken from Endress et al. (1996) and Williams (2002).

(19) Shape of the upper extension of the connective: **0** = **obtuse**; **1** = **deltoid**; **2** = **filamentous**. Williams (2002) coded the absence/presence of an apical connective without recognizing differences among them. Our personal observations show that in all the studied species of the tribe, the upper extension of the connective is always present, but it differs in form among the species. Shapes are coded according to Radford (1986).

(20) Apical connective color tone: **0** = **clear**; **1** = **dark**. This character has been used only in a taxonomic treatment (Fallen, 1983). Personal observations indicate that the presence of a dark tone in the apical connective could be the result of the oxidation of some chemical compound(s) and it is a constant condition shared by several species.

(21) Apical connective arrangement: **0** = **free**; **1** = **connate**. The fusion of the apical connective of the anthers has been mentioned for some species of *Cerbera* (Pichon, 1948a; Leeuwenberg, 1999) and *Thevetia* (Gensel, 1969; Fallen, 1986), but it has not been used in cladistic analyses. Our observations corroborate the previous works, and, therefore, we include this character for the first time in a phylogenetic context.

(22) Pollen grain diameter (μm): **0** = **20–50**; **1** = **50–80**; **2** = **80–120 (additive)**. Several authors (Pire, 1989; Roubik & Moreno, 1991; Williams, 1998, 2002) have regarded the pollen diameter as a useful character to identify and suggest relationships among genera. Van der Ham et al. (2001) considered two states in their cladistic analysis: “**0** = small (3 μm), **1** = big (6 μm),” while Williams (2002) recognized three states: “**0** = 20–35 μm , **1** = 40–75 μm , **2** = 75–100 μm .” Here we assigned the intervals for the character states in agreement with the results of the statistical analysis (see “Material and Methods”). The character was coded as additive because it is possible to hypothesize a transitional series of increase or decrease.

(23) Tectum continuity: **0** = **eutectate (perforate)**; **1** = **subtectate (heterofoveolate to microreticulate)**. Endress et al. (1996) coded this character with six states. Nevertheless, the states they proposed considered a wider sampling that included more hierarchical levels. In addition, we believe that, in their coding, they included as the same attributes conditions that could be considered as different characters. For instance, they regarded as part of the tectum continuity attributes that we believe to be related to ornamentation (scabrate, undulate, verrucate, etc.). Here, we decided to recognize only the condition related to the continuity of the tectum, which in our sampling can be eutectate (imperforate or perforate) or subtectate (foveolate or reticulate). In our sampling, the ornamentation is more or less constant within the species.

(24) Exine thickness (μm): **0** = **1.0–2.0**; **1** = **3.0–4.0**. This character is used widely in palyno-taxonomic works, but it has not been included in cladistic analyses of the family. Even though it is variable within species, our

observations show that within Plumerieae, the exine thickness has constant intervals at a specific level with a clear gap between the intervals, so it is not necessary to do a statistical analysis to recognize the two character states.

(25) Presence of endofissures in the nexine: **0** = **no**; **1** = **yes**. Endress et al. (1996) used this character to describe patterns of the inner exine, considering four states: “**0** = smooth, **1** = finely granulate to verrucate, **2** = coarsely granular to verrucate, **3** = with fissures.” We consider only the absence/presence of fissures (endocracks) because, although they are easily appreciable under optical and scanning electronic microscopy (displaying the same irregular pattern in *Cascabela* and *Thevetia*), at this moment we do not have observations for the inner ultrastructure that allow us to define variants in texture.

(26) Presence of a depression in the mesocolpium: **0** = **no**; **1** = **yes**. The coding of this character was taken from Endress et al. (1996).

(27) Presence of infrastaminal appendages: **0** = **no**; **1** = **yes**. The coding of this character was taken from Endress et al. (1996) and Williams (2002).

(28) Shape of infrastaminal appendages: **0** = **cylindrical**; **1** = **quadrangular**; **2** = **semicircular**. The character is included for the first time in a cladistic analysis, based on personal observations that show that the shape of the infrastaminal appendages is constant within species and variable amongst them, revealing its potential phylogenetic information. The definition of states follows the terminology of Radford (1986).

(29) Presence of ornamentation on the infrastaminal trichomes: **0** = **no** (Fig. 4E); **1** = **yes** (Fig. 4F–H). The internal trichomes of the flower have not been widely studied in detail within Apocynaceae. Bruyns (2000) reported the microscopic characteristic of trichomes on the corolla of species from tribe Ceropegieae, coding the absence/presence and the ornamentation of modified trichomes. Here we adjust these attributes according to our observations. The presence/absence of ornamentation is constant within species.

(30) Infrastaminal trichome ornamentation pattern: **0** = **verrucose** (Fig. 4F); **1** = **discontinuous striations** (Fig. 4G); **2** = **continuous striations** (Fig. 4H). Within the species that display ornamentations on the infrastaminal trichomes (previous character), the pattern of the ornamentation is also constant within species and it varies amongst them. The species that lack ornamentation on the infrastaminal trichomes were coded as inapplicable (-).

(31) Carpel grouping: **0** = **congenitally syncarpous**; **1** = **postgenitally syncarpous**; **2** = **apocarpous**; **3** = **partially syncarpous**. The character and its states were modified according to our sampling from Endress et al. (1996).

(32) Ovary position: **0** = **superior**; **1** = **semi-inferior**. This character has a great taxonomic importance, and it has not been used in cladistic analyses. *Himatanthus*, *Mortoniella*, and *Plumeria* are the only genera in the tribe that share a semi-inferior ovary. Pichon (1948a, 1950a) and Leeuwenberg (1994) suggested that this character could point to a possible relationship among those genera.

(33) Number of ovules per carpel: **0** = **2**; **1** = **4–6**; **2** = **20–40 (additive)**. The number of ovules per carpel is a character that has not been used in previous phylogenetic works. It has constant intervals within species and gaps amongst them, which allow us to propose the states even without having to do descriptive statistics. This character is considered as additive, suggesting a hypothesis of logic transition to increase or reduction of ovule number.

(34) Presence of nectary: 0 = no; 1 = yes (Fig. 4I, J). The coding of this character and its states is taken from Endress et al. (1996) and Sennblad et al. (1998). Several authors (Woodson, 1938a; Standley & Williams, 1958) did not report a nectary in *Cameraria latifolia*, but our observations revealed that an external portion of the ovary wall has differences in coloration and cellular type. This tissue is here interpreted as nectary because its characteristics resemble the ones for other species where a nectary is generally reported.

(35) Stigmata shape: 0 = semispherical; 1 = cylindrical to fusiform (Fig. 4K); 2 = conic (Fig. 4L, M). The term “stigmata” was used by Boiteau and Allorge (1978) referring to the sterile apical part of the stigmatic head. This structure has cellular differences with respect to the rest of the stigma and fulfills a particular function (Fallen, 1986). It is the first time that this character is employed in a cladistic analysis, and we recognize three characters that represent different attributes and potential homologies within the structure: shape (35), position (36), and cell shape (37). The shape of the stigmata is constant in all the species checked. The cylindrical or fusiform shapes occupy only about one third of the stigma, while the conical shape is a massive structure that constitutes half or more than half of stigma.

(36) Relative position of the stigmata: 0 = not convergent (Fig. 4K, L); 1 = convergent (Fig. 4M). Among the species in the tribe, at least two constant patterns of stigmata arrangement can be distinguished. In not-convergent stigmata, the lobes are parallel and independent, not touching each other. In contrast, in convergent stigmata, the lobes are in full contact with each other, sometimes even fused at the base.

(37) Stigmata cells shape: 0 = filiform (Fig. 4N); 1 = conic (Fig. 4O); 2 = irregularly flattened (Fig. 4P). The shape of the stigmata cells presents different patterns amongst different species, which can unambiguously be defined as different states of the character.

(38) Secretory region shape: 0 = cylindrical to elliptic (Fig. 4K, L); 1 = lobulate (Fig. 4M). This character was used by Boiteau and Allorge (1978) to differentiate subfamily Plumerioideae from Tabernaemontanoideae, but it has not been used in phylogenetic analyses. Here, we adopt the proposal of those authors because, within the tribe, there are clear and constant differences in the shape of the secretory region.

(39) Receptivity pattern: 0 = level 1; 1 = level 2. This character follows the proposal of Fallen (1986) and Endress et al. (1996).

(40) Fruit shape in cross-section: 0 = elliptic to circular; 1 = strongly compressed. This character was used in cladistic analyses for other families within the order Gentianales (Bremer, 1992; Ochoterena, 2000). The character is implemented here because the states are easy to recognize and not ambiguous. The compressed fruits differ from the circular or elliptical ones by a clear compression on both planes.

(41) Shape of non-compressed fruits: 0 = fusiform; 1 = linear; 2 = subspheroid (Fig. 1B); 3 = reniform (Fig. 1F). Klackenberg (1998), when considering the fruit margin, recognized two character states: “0 = follicles with straight margin” and “1 = follicles with sinuate margin.” Liede (1994) instead used the entire form of the fruit, also recognizing two states: “0 = obclavate” and “1 = fusiform.” Here we adjust these proposals according to the shapes observed within Plumeriaceae. The linear fruits have a more or less constant diameter along them, only thinned in the apical

part; the fusiform fruits are thinner at both ends. The reniform and subspheroid shapes do not have a uniform diameter along the length of the fruit; the reniform shape is wider than long and clearly displays two lobes.

(42) Exocarp color: 0 = blue; 1 = brown; 2 = red; 3 = black. The characteristic color of the fruits was employed by Williams (2002), coded as: “0 = brown,” “1 = red,” and “2 = black.” We adjust the character states according to our sampling. We consider that the colors of the fruit represent valid homology hypotheses because they appear to be due to the presence of specific compounds.

(43) Presence of lenticels on the exocarp: 0 = no (Fig. 1F); 1 = yes (Fig. 1B). We believe that this character has potential phylogenetic information because its presence or absence seems to be constant within species and variable among them. The lenticels on the exocarp can be seen even when the fruits are not mature.

(44) Mesocarp consistency: 0 = woody; 1 = coriaceous; 2 = fleshy; 3 = spongy (Fig. 4R, S). Endress et al. (1996) considered that the variation of fruit consistency is due to the mesocarp, an idea that we support. These authors coded the texture as: “0 = fleshy” or “1 = dry or woody.” Although it is possible that some properties of the texture can be modified when the fruits dry, the characteristics that remain suggest differences in the cellular type of the mesocarp among species. We consider that it is possible to distinguish more than two characters states, from Endress et al.’s “dry or woody” condition. Potgieter and Albert (2001) considered that the fruits of *Cerbera manghas*, *C. odollam*, *Cerberiopsis candelabra*, and *Thevetia peruviana* (= *Cascabela thevetia*) have a sclerified mesocarp; our observations from *Cascabela* and *Cerbera* indicate that the sclerified consistency corresponds to the endocarp (see character 47), and the middle layers have a fleshy and spongy texture, respectively. On the other hand, *C. candelabra* does not have sclerified layers.

(45) Endocarp texture: 0 = non-sclerified; 1 = sclerified thin; 2 = sclerified thick (stony) (Fig. 4R). Endress et al. (1996) coded this character with two states: “0 = non-sclerified” and “1 = sclerified.” We consider that among the genera that have fleshy mesocarp (those coded as sclerified by Endress et al.), it is possible to recognize two states: the fruits of *Cerbera* and *Cascabela* have a thicker and more rigid endocarp than those of *Thevetia*. Strictly speaking, the definition for “stony” implies the presence of stone cells (Font Quer, 1982), but given the lack of anatomical studies, we provisionally assess this state by the rigidity and the thickness of the structure, because we believe that the differences in texture among those genera could be due to a different cellular nature. The species with woody mesocarp were coded as inapplicable to avoid weighting of characters, because in that case, both layers (mesocarp and endocarp) have the same texture, a condition that we believe that could be correlated.

(46) Endocarp external surface: 0 = smooth; 1 = ornamented (Fig. 4Q–S). In tribe Plumeriaceae, most of the species have a smooth endocarp, but in the species of *Cerbera* and *Thevetia*, this layer is ornamented.

(47) Endocarp forming a network with the mesocarp: 0 = no; 1 = yes (Fig. 4Q–S). The presence of endocarp forming a network with the mesocarp is not common among the species of Apocynaceae. Potgieter and Albert (2001) considered that sclerified fibers of the mesocarp were responsible for the rigid consistency of *Cerbera*’s fruits, but our results show that these fibers arise from the endocarp and surround the spongy mesocarp, forming a network. The species with woody mesocarp were coded as inapplicable (see character 45).

(48) Endocarp presentation (Fig. 3): **0 = single; 1 = segmented.** This character has a great taxonomic importance, but it had never been used in cladistic analyses. Within Plumerieae, only the species of *Thevetia* have a segmented endocarp.

(49) Relative time of fruit dehiscence: 0 = dehiscient when mature; 1 = tardily dehiscient. Williams (2002) used this character, coding the fruits as dehiscient or indehiscient. Here we prefer to contrast relative times of dehiscence, because some fruits considered as indehiscient open after maturity, a process referred to as "delayed dehiscence" (Roth, 1977). This is the case of the drupaceous fruits of *Cascabela*, *Cerbera*, and *Thevetia* and the samaroid fruits of *Cameraria* and *Cerberiopsis*.

(50) Presence of a wing on the seed: 0 = no; 1 = yes. Endress et al. (1996) considered three states for this character: "0 = naked, 1 = winged, 2 = with cilia or hairs." Here we included the conditions present within Plumerieae.

(51) Seed wing position: 0 = concentric; 1 = at both ends; 2 = lateral opposite to the micropyle; 3 = lateral surrounding the micropyle. The position of the wing was used by Potgieter and Albert (2001), who recognized three states: "0 = not circumlate, 1 = circumlate, 2 = naked." Our observations let us recognize two variations within the not circumlate (concentric) wings, which can be established as distinct hypotheses of primary homology. In some taxa, the wing can develop opposite to the micropyle (e.g., *Plumeria*), while in others, they develop in the region of the micropyle, covering it (*Cascabela*, *Cerberiopsis*, and *Thevetia*). Taxa without seed wings were coded as inapplicable (-).

(52) Continuity of the margin of the seed wing: 0 = entire; 1 = denticulate. The characteristics of the seed wing margin were used by Pichon (1949) to diagnose the different tribes and subtribes within the family. Here we employ two of his proposals according to the states present in our sampling. Taxa without seed wings were coded as inapplicable (-).

(53) Testa texture: 0 = sclerous; 1 = coriaceous; 2 = papyraceous; 3 = crustaceous. Pichon (1949) also considered for his classification characteristics of the texture of the testa. Here we modify his proposal to include the conditions present within the tribe. The character states can be easily distinguished, and their properties seem to be maintained after drying of the specimens.

(54) Degree of embryo compression: 0 = on both sides; 1 = on one side (Fig. 3); **2 = apparently uncompressed** (Fig. 3) (**additive**). The compression of the embryo is implemented for the first time in a phylogenetic analysis. It refers to the shape in cross-section, which is constant within species and variable among them. The embryos with compression in both sides have a more or less linear shape; the embryos with compression have a plane face on one side and a convex face on the other; those without compression have both faces convex, looking like an ellipse. The embryo compression is not directly related to the fruit shape or the texture of the mesocarp (e.g., subspheroidal or fleshy fruits can have compressed or uncompressed embryos).

APPENDIX 4. Taxonomic synopsis.

Family Apocynaceae Juss., Gen. Pl. 143. 1789.

Subfamily Rauvolfioideae Kostel., Allg. Med.-Pharm. Fl. 3: 1054. 1834.

Tribe Plumerieae E. Meyer, Comm. Pl. Afr. Austr. 2: 188. 1838.

Subtribe Plumeriinae Benth. & Hook. f. Gen. Pl. 2: 685. 1876.

Subtribe Allamandinae A. DC., Prodr. 8: 318. 1844.

Subtribe Thevetiinae A. DC., Prodr. 8: 342. 1844.

KEY TO THE *CASCABELA*–*THEVETIA* COMPLEX

- 1a. Flowers with digitiform supracarpal appendages; drupes pear-shaped to subspheroid, exocarp black, mesocarp fleshy, endocarp whole, thick (stony); embryo uncompressed *Cascabela*
- 1b. Flowers with deltoid supracarpal appendages; drupes reniform, exocarp red, mesocarp leathery, endocarp segmented, thin; embryo compressed on one side *Thevetia*

1a. *Cascabela* Raf., Sylva Tellur. 162. 1838.
Thevetia Adans., Fam. Pl. 2: 171. 1763, non *Thevetia* L. *Thevetia* section *Euthetia* K. Schum., in Engler & Prantl, Nat. Pflanzenfam. 4(2): 159. 1895. *Thevetia* section *Yccotli* Kuntze, in Post & Kuntze, Lex. Gen. Phan. 558. 1903. TYPE: *Cascabela peruviana* (Pers.) Raf., Sylva Tellur. 162. 1838 [= *Cascabela thevetia* (L.) Lippold].

Trees or shrubs with milky latex. Leaves alternate, sessile or petiolate; laminae membranaceous to subleathery, with or without conspicuous secondary venation. Inflorescences terminal, corymbs compound. Sepals with colletes; corolla yellow or orange, hypogynous, funnelform, lobes sinistrorse-contorted, extended; supracarpal appendages digitiform, villous; anthers supported by ribs, latrorse, included, agglutinated on the stigma, apical connective deltoid, dark, fused; infrastaminal appendages semicircular, hirsutulous; ovary partially syncarpic, glabrous, ovules 2 per carpel, marginal placentation, stigma conical, base 10-lobed; nectary annular. Fruit as pear-shaped to subspheroid drupes, exocarp black, with or without lenticels, mesocarp fleshy, endocarp whole, thick (stony), smooth; seeds winged, fimbriate, testa crustaceous, embryo uncompressed.

KEY TO SPECIES OF *CASCABELA*

- 1a. Leaf lamina obovate to oblanceolate.
 - 2a. Leaves membranaceous to subleathery, glabrous, inconspicuous secondary venation; bracts glabrous; drupes not lenticellate 1. *C. gaumeri*
 - 2b. Leaves leathery, hirsute to tomentose, conspicuous secondary venation; bracts tomentose; drupes lenticellate 2. *C. ovata*
- 1b. Leaf lamina linear to lanceolate.

- 3a Lamina of the leaves with inconspicuous secondary venation; corolla tube 1.0–1.8 cm.
1a. Leaves sessile, lamina linear; inflorescence peduncles 0.8–3.0 cm; bracts persistent; corolla tube internally glabrous 3. *C. pinifolia*
1b. Leaves petiolate, lamina lanceolate to elliptic; inflorescence peduncles 0.3–0.9 cm; bracts deciduous; corolla tube internally pubescent
. 1. *C. thevetia*
3b. Lamina of the leaves with conspicuous secondary venation; corolla tube 2.0–3.0 cm 5. *C. thevetioides*

1. *Cascabela gaumeri* (Hemsl.) Lippold, Feddes Repert. 91: 53. 1980. Basionym: *Thevetia gaumeri* Hemsl., Icon. Pl. 1517. 1886. TYPE: Mexico. Quintana Roo: Cozumel Island, 1885, *G. F. Gaumer* 7 (holotype, F not seen, F photo MEXU!). Figure 1C.

Thevetia spathulata Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 383. 1898. TYPE: Mexico. Yucatán: Yucatán, common at the port of Silam, Apr. 1895, *G. F. Gaumer* 678 (lectotype, designated by Morales (2005, 43: 175), MO not seen, MO photo MO!; isotype, F).

Thevetia steerei Woodson, Amer. J. Bot. 22: 685. 1935. TYPE: Mexico. Yucatán: in low forest, Progreso, 11–15 Aug. 1932, *W. Steere* 3056 (holotype, MO not seen, MO photo MO!; isotype, NY not seen, NY photo NY!).

Trees 2.0–13.0 m. Leaves petiolate; laminae oblanceolate, 10.0–12.0 × 1.9–3.0 cm, membranaceous to subleathery, glabrous, inconspicuous secondary venation. Inflorescences with 10 or more flowers; peduncles 2.0–5.0 cm, glabrous; bracts ovate, 4.0–5.7 × 3.0–4.0 mm, persistent, glabrous. Flowers with pedicels 1.6–3.5(–4.2) cm, glabrous; sepals ovate, 0.5–1.3 × 0.3–0.4 cm, glabrous; corolla greenish yellow, tube 1.5–1.7 cm, 3.0 mm diam., internally glabrous, throat 1.1–1.3 cm, 1.5 cm diam., lobes oblong, 2.6–3.0 × 2.0 cm; anthers 2.0 × 1.5 mm; ovary 1.6–1.9 × 1.7–1.9 mm, glabrous, style 1.0–1.5 cm, stigma 2.0–2.3 × 2.5 mm. Drupes 2.0–2.8 × 2.5–3.0 cm, not lenticellate; seeds 1.3–2.0 × 1.0–1.5 cm.

Distribution. Mexico (Campeche, Guerrero, Quintana Roo, Veracruz, and Yucatan) and Central America (Belize, Guatemala, and Nicaragua).

Discussion. *Cascabela gaumeri* and *C. thevetia* are morphologically very similar, but they can be easily distinguished by the shape of the laminae (oblanceolate in *C. gaumeri* vs. lanceolate to elliptic in *C. thevetia*), the hairs in the corolla tube (absent in *C. gaumeri* vs. present in *C. thevetia*), and the color of the flowers (greenish yellow in *C. gaumeri* vs. yellow or orange in *C. thevetia*).

Selected specimens examined. BELIZE. **Corozal:** Basil Jones ambergris, 15 km N de San Pedro, *S. Torre* 308

(MEXU). GUATEMALA. **Petén:** Dos Lagunas, Km 7 on Ixcario road, *E. Contreras* 8397 (MEXU, NY). MEXICO. **Campeche:** Km 6 rumbo a Nuevo Becal, *Bucab* 103 (MEXU). **Guerrero:** Cerro Alquitrán, ca. del pueblo de Mazatlán, *Schwabe* s.n. (MEXU). **Quintana Roo:** 0.7 km N del poblado Sabana de San Francisco, *D. Álvarez* 9426 (MEXU). **Veracruz:** Cerro de Carbón, *M. Cortés* 412 (MEXU). **Yucatán:** Orilla del camino Señor-San Antonio, *M. Correa* 260 (MEXU).

2. *Cascabela ovata* (Cav.) Lippold, Feddes Repert. 91: 53. 1980. Basionym: *Cerbera ovata* Cav. Icon. 3: 35, pl. 270. 1796. *Thevetia ovata* (Cav.) A. DC., Prodr. 8: 344. 1844. TYPE: Mexico. Nueva España (holotype, MA not seen, MA photo MA!).

Cerbera alliodora Roem. & Schult., Syst. Veg. 4: 798. 1819. Syn. nov. *Cascabela alliodora* (Roem. & Schult.) Lippold, Feddes Repert. 91: 53. 1980. *Thevetia alliodora* (Roem. & Schult.) Allorge, Succulentes 21: 27. 1998. TYPE: Mexico. Guerrero: “inert Zumpango et Mescalám, in convalli Zopilote,” [Apr. 1803], *F. W. H. A. Humboldt* & *A. J. A. Bonpland* s.n. (holotype, P not seen, P photo NY!).

Cerbera cuneifolia Kunth, Nov. Gen. Sp. 3: 224. 1818 [1819]. *Thevetia cuneifolia* (Kunth) A. DC., Prodr. 8: 344. 1844. TYPE: Mexico. Guerrero: “inert Zumpango et Mescalám, in convalli Zopilote,” [Apr. 1803], *F. W. H. A. Humboldt* & *A. J. A. Bonpland* s.n. (holotype, P not seen, P photo MEXU!).

Thevetia cuneifolia (Kunth) A. DC. var. *andrieuxii* A. DC., Prodr. 8: 344. 1844. TYPE: Mexico. [México-Morelos]: in Mexico ad Gonacatepec, *G. Andrieux* 254 (holotype, G-DC!; isotype, P not seen).

Thevetia plumeriifolia Benth., Bot. Voy. Sulphur 124, t. 43. 1845. *Cascabela plumeriifolia* (Benth.) Lippold, Feddes Repert. 91: 53. 1980. TYPE: Honduras. Gulf of Fonseca, *S. Sinclair* s.n. (lectotype, designated by Nelson (1996, 44: 60), K not seen, K photo K!).

Trees 2.0–10.0 m. Leaves petiolate; laminae obovate to oblanceolate, 5.5–17.5 × 2.5–8.5 cm, leathery, hirsute to tomentose, with conspicuous secondary venation. Inflorescences with 5 to 15 flowers; peduncles 0.5–1.3 cm, hirsute to glabrate; bracts ovate, (3.0–)5.0–7.0 × 2.0–6.0 mm, persistent, tomentose. Flowers with pedicels 2.4–7.0 cm, hirsute to glabrate; sepals ovate, 0.5–1.2 × 0.3–0.5 cm, glabrous; corolla yellow, tube 0.8–2.5 cm, 4.0 mm diam., internally glabrous, throat (0.9–)1.3–2.5 cm, 2.0–2.3 cm diam., lobes oblong, (1.2–)2.4–4.5 × (1.0–)2.2–2.5 cm; anthers 2.0 × 1.0 mm; ovary 2.0 × 4.0–5.0 mm, glabrous, style 1.5 cm, stigma 1.5–2.0 × 2.5 mm. Drupes 2.0–3.7 × 2.8–5.5 cm, lenticellate; seeds 1.8–2.0 × 1.8 cm.

Distribution. Mexico (Chiapas, Colima, Durango, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, and Zacatecas), Costa Rica, El Salvador, Guatemala, Honduras, and Nicaragua.

Discussion. *Cascabela ovata* is easy to recognize by the obovate to oblanceolate leaves, with leathery

consistency, tomentose indumentum, and conspicuous secondary venation.

Selected specimens examined. COSTA RICA. **Guanacaste:** Península de Nicoya, bejuco la Isleta, *Q. Jiménez 1651* (NY). EL SALVADOR. **La Libertad:** Puente Sihuatepeque, carr. Litoral de occidente, *Montalvo 6376* (NY). GUATEMALA. **El Quiché:** Río Blanco, near village of Río Blanco, *L. Williams 22455* (NY). HONDURAS. **Morazán:** Drainage of the Río Yeguaré, Casa Blanca, *Glassman 1819* (NY). MEXICO. **Chiapas:** 8 km W de Tuxtla Gutiérrez, al W de la colonia Juan Crispín, *Reyes-García 1955* (MEXU). **Colima:** Manzanillo, *E. Palmer 1069* (NY). **Durango:** 6 km S de Huazamota, *S. González 2403* (MEXU). **Guerrero:** Sochopala, *Bruff 1107* (MEXU). **Jalisco:** Chimalistán, *R. Hernández 9420* (MEXU). **México:** Dolores, *Matuda 31264* (MEXU). **Michoacán:** 5–6 km NE de la desviación a Tuzantla, 14 km NE de Tiquicheo, *F. Chiang 536* (MEXU). **Morelos:** Brecha Xicatlán a Xicatlacotla, *Quezada 1699* (MEXU). **Nayarit:** Colorado de la Mora, *Benítez 3107* (MEXU). **Oaxaca:** 50 mi. S of Oaxaca on hwy., *Dwyer 14360* (MEXU). **Sinaloa:** 30 km NE de Culiacán, rumbo a la presa El Comedero, *C. Ortiz 327* (MEXU). **Zacatecas:** W de Pueblo Viejo, Cerro de Piñones ladera E, casa de J. Ayala, *Balleza 8482* (MEXU). NICARAGUA. **Boaco:** Km 101 carr. Juigalpa, el Papayal, *P. Moreno 3629* (MEXU).

- 3. *Cascabela pinifolia*** (Standl. & Steyererm.) Alvarado-Cárdenas & Ochot.-Booth, comb. nov. Basionym: *Thevetia peruviana* (Pers.) K. Schum. var. *pinifolia* Standl. & Steyererm., Amer. Midl. Naturalist 36: 185. 1946. *Thevetia pinifolia* (Standl. & Steyererm.) J. K. Williams, Sida 17: 187. 1996. TYPE: Mexico. Michoacán: trail from Apatzingan to Tacitaro, 7 Aug. 1940, *W. C. Leavenworth 505* (holotype, F not seen, F photo MEXU!; isotypes, GH not seen, NY not seen, NY photo NY!).

Trees or shrubs 1.8–5.0 m. Leaves sessile; laminae linear, 8.0–20.0 × 0.1–0.3 cm, membranaceous, glabrous to hirsute, inconspicuous secondary venation. Inflorescences with 6 to 14 flowers; peduncles 0.8–3.0 cm, hirsute to glabrate; bracts ovate, 3.1–4.9(–6.0) × 3.0–4.5 mm, persistent, hirsutulous. Flowers with pedicels 1.0–2.7 cm, glabrous; sepals ovate, 0.5–1.1 × 3.0–4.0 mm, glabrous; corolla yellow, tube 1.0–1.8 cm, 3.0–4.0 mm diam., glabrous inside, throat 0.9–1.1 cm, 1.5–2.0 cm diam., lobes oblong, 2.4–3.7 × 2.0 cm; anthers 1.3–2.0 × 1.2 mm; ovary 2.5–3.2 × 3.0 mm, glabrous, style 1.2–1.5 cm, stigma 2.0–2.4 × 3.0 mm. Drupes 2.5–3.0 × 4.0–5.0 cm, lenticellate; seeds 1.0–1.8 × 1.0 cm.

Distribution. Endemic of Mexico in the states of Guerrero, México, Michoacán, and Puebla.

Discussion. Occasionally *Cascabela pinifolia* is incorrectly determined as *C. thevetia*, but they can be easily distinguished by the shape of the laminae (linear in *C. pinifolia* vs. lanceolate to elliptic in *C. thevetia*), the indumentum on the bracts (hirsutulous

in *C. pinifolia* vs. glabrous in *C. thevetia*), and the hairs in the corolla tube (absent in *C. pinifolia* vs. present in *C. thevetia*).

Selected specimens examined. MEXICO. **Guerrero:** 29 km SW de Zirandaro, cam. Guayameo, *E. Martínez 1336* (NY). **México:** Bejucos, *G. Hinton 3792* (NY). **Michoacán:** En Las Colonias, *E. Martínez et al. 3639* (MEXU). **Puebla:** Paraje Cerro Gordo, 1 km NE de la cabecera municipal, *Castañeda 41* (MEXU).

- 4. *Cascabela thevetia*** (L.) Lippold, Feddes Repert. 91(1–2): 52. 1980. Basionym: *Cerbera thevetia* L., Sp. Pl. 1: 209. 1753. *Cerbera peruviana* Pers., Syn. Pl. 1: 267. 1805. *Thevetia neriifolia* Juss. ex Steud., Nomencl. Bot. (ed. 2). 180. 1821. *Cascabela peruviana* (Pers.) Raf. Sylva Tellur. 162. 1838. *Thevetia linearis* Raf., Sylva Tellur. 91. 1838. *Thevetia peruviana* (Pers.) K. Schum., in Engler & Prantl, Nat. Pflanzenfam. 4: 159. 1895. *Thevetia thevetia* (L.) Millsp., Field Mus. Nat. Hist. Bot. Ser. 2: 83. 1900. TYPE: America. s. loc. et coll. (holotype, Herb. Linn. 298.1, BM not seen). Figure 1D.

Thevetia yccotli var. *glabra* A. DC., Prodr. 8: 343. 1844. Syn. nov. TYPE: Mexico. Tamaulipas: Tampico, 1827, *J. L. Berlandier 189* (holotype, G-DC!; isotype, P not seen. P image MEXU!).

Trees or shrubs 2.0–8.0 m. Leaves petiolate; laminae lanceolate to elliptical, 8.0–16.3 × 0.5–1.4 cm, membranaceous, glabrous, with inconspicuous secondary venation. Inflorescences with 6 to 8 flowers; peduncles 0.3–0.9 cm, glabrous; bracts ovate, 1.8–4.0 × 1.0–2.0 mm, deciduous, glabrous. Flowers with pedicels 2.5–3.0 cm, glabrous; sepals ovate to lanceolate, 0.5–1.3 × 0.2–0.4 cm, glabrous; corolla yellow or orange, tube 1.2–1.7 cm, 3.0–5.0 mm diam., internally pubescent, throat 0.8–1.4 cm, 1.2–1.4 cm diam., lobes oblong, 2.5–3.5 × 1.7–2.5 cm; anthers 2.0–2.5 × 1.5 mm; ovary 4.0 × 3.0 mm, glabrous, style 1.0–1.2 cm, stigma 2.0–3.0 × 2.5–3.0 mm. Drupes 2.5–3.5 × 2.1–4.5 cm, sometimes lenticellate; seeds 1.0–1.2 × 1.0 cm.

Distribution. Mexico (Campeche, Chiapas, Guerrero, Hidalgo, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, and Yucatán), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama), South America (Bolivia, Brazil, British Guiana, Colombia, Ecuador, Perú, and Venezuela), and the Antilles (Bahamas, Cuba, Dominican Republic, Haiti, Jamaica, and Puerto Rico). Today cultivated in the tropics of the world.

Discussion. This species is frequently confused with *Cascabela thevetioides* because both have lanceolate

leaves. However, they can be distinguished by the secondary veins (inconspicuous in *C. thevetia* vs. exposed in *C. thevetioides*), the leaf indumentum (glabrous in *C. thevetia* vs. tomentose in *C. thevetioides*), and the corolla tube size (1.2–1.7 cm in *C. thevetia* vs. 2.0–3.0 cm in *C. thevetioides*). In the Linnaean herbaria there are other specimens that can be associated with *C. thevetia*: Linn 296.4 (LINN not seen, LINN photo MEXU!) and *S-Linn. IDC 105.5* (S not seen, S photo S!). Morales (2005) considers that the holotype of this species is *Herb. Linn. 298.1* (BM), but there is no discussion supporting this decision. We are provisionally accepting his choice, mainly because we did not have access to that specimen, but we consider that it should be reviewed having all the material at hand.

Selected specimens examined. BAHAMAS: s. loc., 13 Apr 1978, *Braee 243 (516)* (NY). BELIZE. **Cayo:** El Cayo and vicinity, *Chanek 33* (MEXU). BOLIVIA. **Santa Cruz:** región de Lomerío, comunidad de San Antonio, cerca de la iglesia, *M. Toledo 291* (NY). BRAZIL. Villa Maria, *O. Kuntze s.n.* (NY). BRITISH GUIANA. s. loc., *Jenman 48-2* (NY). COLOMBIA. **Antioquia:** El Bagre, along road near airport, *Zarucchi 3260* (NY). COSTA RICA. **San José:** San Pedro, Ciudad Universitaria, *Döbbeler 571* (MEXU). CUBA. Ensenada de Mora, river valley, *N. Britton 12954* (NY). DOMINICAN REPUBLIC. Vicinity Río Arriba del Norte, N of San Juan, *R. Howard 9301* (NY). ECUADOR. In collibus prope Guayaquil, *Mille 60* (NY). EL SALVADOR. **Sonsonete:** vicinity of Nahulingo, *P. Standley 22012* (NY). GUATEMALA. **Santa Rosa:** Cenaguilla, *Heyden 3995* (NY). HAITI. Morne l'Hospital, Fortan Prince, *Holdridge 102* (NY). HONDURAS. Puerto Sierra, *P. Wilson 317* (NY). JAMAICA. **Saint Andrew:** above Mahogany Vale foot bridge, *Yuncker 18325* (NY). MEXICO. **Campeche:** 2 km W de Calakmul, camino a la Laguna, *E. Martínez et al. 27641* (MEXU). **Chiapas:** Escuintla, *Matuda 16715* (MEXU). **Guerrero:** Costa Verde, *Laugman 3325* (MEXU). **Hidalgo:** Límites de Hidalgo-San Luis Potosí, hacia Tamazuchale, *R. Hernández 3922* (MEXU). **Michoacán:** en Las Colonias, *J. Soto 4966* (MEXU). **Nayarit:** La Quita La Concordia, en el campamento Balleto, *O. Téllez 4139* (MEXU). **Oaxaca:** San Juan Atepec, 8 km de la terracería al poblado, hacia Abejones, en el Puente de Río Grande, *Alvarado-Cárdenas et al. 38* (MEXU). **Puebla:** near Coxcatlán on Cerro Ajuereado and in the adjacent valley, *Smith. C. 3640* (NY). **Querétaro:** Orilla del Río Santa María, 4 km de las mesas de Agua Fria, *A. Herrera 128* (MEXU). **Quintana Roo:** en San Miguel Cozumel, lote baldío, *Cabrera 13622* (MEXU). **San Luis Potosí:** Rascon, *Pringle 4107* (NY). **Tabasco:** Carr. W-O en el Aserradero quemado, *Calzada 2375* (NY). **Tamaulipas:** Sierra Guatemala, 1 air mile N of the square at Gómez Farias on road to Rancho del Cielo, *Sullivan 683* (NY). **Veracruz:** 2 km NE of Emiliano Zapata (Carrizal), 1 km S of hwy. Mex 140, *Hansen 7518* (NY). **Yucatán:** 1 km al SE de Tecax, sobre la carr. a Chetumal, *Cabrera 11328* (MEXU). NICARAGUA. **Chontales:** 2–3 km NE de Cuapa, *Nee 28477* (NY). PANAMA. Diablo, *Blum 3987* (NY). PERU. **Cajamarca:** ca. 35 km E of Pucara, beside Río Huancabamba, *A. Gentry 22757* (NY). PUERTO RICO. Fajardo, *Sintenis 1650* (NY). VENEZUELA. **Caracas:** Los Chaguar-amos, *Ysalerly 3* (NY).

5. *Cascabela thevetioides* (Kunth) Lippold, Feddes Repert. 91: 53. 1980. Basionym: *Cerbera thevetioides* Kunth, Nov. Gen. Sp. 3: 223. 1818 [1819]. *Thevetia thevetioides* (Kunth) K. Schum., Nat. Pflanzenfam. 4(2): 159. 1895. TYPE: Mexico. Guerrero: Taxco, [Apr. 1803], *F. W. H. A. Humboldt & A. J. A. Bonpland s.n.* (holotype, P not seen, P photo MEXU!). Figure 1A, B.

Thevetia yccotli var. *yccotli* A. DC. Prodr. 8: 343. 1844. TYPE: Mexico. [México?]; In Mexico ad Gonacatepec, *G. Andrieux 253* (holotype, G-DC!; isotype, P not seen).

Trees 2.5–10.0 m. Leaves petiolate; laminae lanceolate, 6.0–14.0 × 0.5–1.3 cm, membranaceous, glabrous to tomentose, with conspicuous secondary venation. Inflorescences with 10 to 18 flowers; peduncles 0.6–2.1 cm, glabrous; bracts lanceolate to ovate, 0.4–1.1 × 3.0–4.0 mm, deciduous, glabrous. Flowers with pedicels 1.2–2.5 cm, glabrous; sepals ovate to lanceolate, 0.6–1.3 × ca. 0.5 cm, glabrous to hirsutulous; corolla yellow, tube 2.0–3.0 cm, 3.0–5.5 mm diam., internally glabrous, throat 1.2–1.9 cm, 1.0–1.8 cm diam.; lobes oblong-obovate, 4.0–5.3 × 3.0–3.5 cm; anthers 2.0–2.8 × 1.0–1.5 mm; ovary 2.5–4.0 × 2.0–2.5 mm, glabrous, style 1.8–2.0 cm, stigma 2.3–2.5 × 2.6–3.0 mm. Drupes 2.3–4.5 × 3.0–6.5 cm, lenticellate; seeds 1.5–1.8 × 1.5–2.0 cm.

Distribution. Endemic of Mexico in the Distrito Federal and the states of Guanajuato, Guerrero, México, Michoacán, Morelos, Oaxaca, Puebla, and Querétaro.

Discussion. This species is frequently confused with *Cascabela thevetia*, because both species have lanceolate leaves. However, they can be distinguished by the presentation of the secondary veins (exposed in *C. thevetioides* vs. inconspicuous in *C. thevetia*), the leaf pubescence (tomentose), to some extent by the flower size (corolla tube 2.0–3.0 cm in *C. thevetioides* vs. 1.2–1.7 cm in *C. thevetia*), and to some degree by the fruit size (drupes 2.3–4.5 × 3.0–6.5 cm in *C. thevetioides* vs. 2.5–3.5 × 2.1–4.5 cm in *C. thevetia*).

Selected specimens examined. MEXICO. **Distrito Federal:** Coyoacán, Jardín Botánico, *García-Mendoza 7194* (MEXU). **Guerrero:** Ajuatetlán, reserva campesina, *Godínez 4* (MEXU). **Guanajuato:** Delgado, cerca de Neutra, *Rzedowski 39849* (MEXU). **México:** Tepetitlán, *F. Ventura 1239* (MEXU). **Michoacán:** Huetamo, en las colonias, *J. Soto 4274* (MEXU). **Morelos:** lava beds near Cuernavaca, *Pringle 6332* (MEXU, NY). **Oaxaca:** Tlacolula, Tlacochahuayo, *Conzatti 4631* (MEXU). **Puebla:** Loma al NE del Calvario de Caltepec, *Tenorio & Alvarado-Cárdenas 20638* (MEXU). **Querétaro:** El Batán, *Argüelles 1055* (MEXU).

***Thevetia* L., Opera Var. 212. 1758, nom. cons.** *Ahouai* Mill., Gard. Dict. Abr. (ed. 4). 1754. *Ahouai* Boehmer, Def. Gen. Pl. 36. 1760. *Ahouai* Adans.

Fam. Pl. 2: 171. 1763. *Thevetia* section *Ahouai* K. Schum. in Engler & Prantl, Nat. Pflanzenfam. 4(2): 159. 1895. *Plumeriopsis* Rusby & Woodson, Ann. Missouri Bot. Gard. 24: 11. 1937. *Ahouai* Pichon, Ann. Mus. Natl. Hist. Nat. 13: 227. 1948. TYPE: *Thevetia ahouai* (L.) A. DC. Prodr. 8: 345. 1844. typ. cons. [*Cerbera ahouai* L., Sp. Pl. 208. 1753].

Shrubs or trees with milky latex. Leaves alternate, petiolate; laminae subleathery, with inconspicuous secondary venation. Inflorescences terminal, corymbs simple, rarely compound. Sepals with colleters; corolla yellow to yellowish sometimes tinted with purple, hypogynous, hippocrateriform or funnellform, lobes sinistrorse-contorted, reflexed or extended; suprstaminal appendages deltoid, villous; anthers supported by ribs, latrorse, including agglutinated on the stigma, apical connective deltoid, dark, fused; infrastaminal appendages quadrangular, hirsutulous. Ovary partially syncarpic, ovules 2 per carpel, marginal placentation, stigma conical, base 10-lobed; nectary annular. Fruits as reniform drupes, exocarp red, with or without lenticels, mesocarp leathery, endocarp segmented, thin, rough; seeds with or without wing, when winged fimbriate, testa crustaceous or leathery, embryo compressed in one side.

KEY TO SPECIES OF *THEVETIA*

- 1a. Leaf lamina lanceolate 2. *T. amazonica*
- 1b. Leaf lamina obovate to spatulate.
 - 2a. Plants 1.5–13.0 m tall; leaves hirsutulous or glabrous; corolla hippocrateriform; seed winged, testa crustaceous 1. *T. ahouai*
 - 2b. Plants 1.0–2.0 m tall; leaves tomentose; corolla funnellform; seeds wingless, testa leathery 3. *T. bicornuta*

1. *Thevetia ahouai* (L.) A. DC., Prodr. 8: 344. 1844. Basionym: *Cerbera ahouai* L., Sp. Pl. ed. 2. 303. 1762. *Plumeriopsis ahouai* (L.) Rusby & Woodson, Ann. Missouri Bot. Gard. 24: 11. 1937. TYPE: Brazil. (lectotype, designated by Leeuwenberg (1993, 127: 94). Hb. Clifford: 76, Plumeria No. 1. BM not seen, BM photo BM!). Figure 1E, F.

Cerbera nitida Kunth, Nov. Gen. Sp. 3: 325. 1819. *Thevetia nitida* (Kunth) A. DC., Prodr. 8: 344. 1844. *Ahouai nitida* (Kunth) Pichon, Ann. Mus. Natl. Hist. Nat. 13: 227. 1948. TYPE: America equatorial [Colombia]: "Crescit ad ostia fluminis et juxta Turbaco Novo-Granatensium." F. W. H. A. Humboldt & A. J. A. Bonpland s.n. (holotype, P not seen, P photo MEXU!).

Thevetia calophylla Miers, Apocyn. S. Am. 20. 1878. TYPE: Venezuela, Valle la Cura, *Mortiz 1158* (holotype, BM!).

Shrubs, rarely trees 1.5–13.0 m. Laminae obovate to elliptical, 8.0–30.0 × 3.8–8.0 cm, hirsutulous or glabrous. Inflorescences with 10 to 18 flowers; peduncles 5.0–15.0 cm, glabrous; bracts ovate, 1.8

4.5 × 2.0 mm persistent, glabrous. Flowers with pedicels 0.8–3.0 cm, glabrous; sepals ovate, 4.0–7.3 × 4.0–5.0 mm, glabrous; corolla yellow to yellowish or white, hippocrateriform, tube 2.0–3.5 cm, 3.0–4.0 mm diam., internally glabrous, lobes oblong-ovate, 0.7–1.8 × 0.6–0.8 cm, reflexed, glabrous; anthers 2.0 × 1.0 mm; ovary 2.0 × 2.0 mm, glabrous, style 1.8 cm, stigma 2.2 × 4.0–5.0 mm. Drupes 2.9–4.0 × 2.0–3.8 cm, not lenticellate; seeds 2.5 × 1.8 cm, winged, testa crustaceous.

Distribution. Mexico (Campeche, Chiapas, Guerrero, Oaxaca, Puebla, Quintana Roo, Tabasco, Veracruz, and Yucatán), Central America (Belize, Costa Rica, Guatemala, Honduras, Nicaragua, and Panama), South America (Colombia and Venezuela), and the Antilles (Cuba). Today cultivated in the tropics of the world.

Discussion. *Thevetia ahouai* is easily recognized by the hirsutulous to glabrous laminae, the corolla lobes reflexed, and the seeds with fimbriate wing and crustaceous testa.

Selected specimens examined. BELIZE. **Cayo:** vicinity of Cuevas S of Millionario, *T. Croat 23561* (NY). COLOMBIA. **Antioquia:** Córdoba 12 km E of Arboletes, along road to Montería, *Zarucchi 4923* (NY). COSTA RICA. **Limón:** Barranca del Colorado, N side betw. town and ocean beach, *D. Stevens et al. 24126* (MEXU). CUBA. **Santa Clara:** Soledad, Cien Fuegos, 25 *J. Jack 8366* (NY). GUATEMALA. **Izabal:** El Estor, La Mina de Exmibal, al E de El Estor, *Tenorio 14579* (MEXU). HONDURAS. **Atlántida:** vicinity of La Ceiba, *Yunker 8284* (NY). MEXICO. **Campeche:** Calakmul, 0.9 km NW de Pioneros del Río, *Calónico 23775* (MEXU). **Chiapas:** Catzaja, Laguna de Catzaja near the hwy. betw. Villa Hermosa and Mérida and E of Bajadas Grandes, *Breedlove 28782* (MEXU). **Guerrero:** San Agustín Oapan, Solar procedente de Iguala, *Hernández del Olmo 618* (MEXU). **Oaxaca:** Cuicatlán, Cafetal El Faro, *Conzatti 3951* (MEXU). **Puebla:** Hueytamalco, El Cerro, *F. Ventura 17876* (MEXU). **Quintana Roo:** 1 km NW del entronque Mérida vía corta, *O. Téllez 2175* (MEXU). **Tabasco:** Arroyo Polo, a la derecha del puente El Coco, *Guadarrama 6568* (MEXU). **Veracruz:** 20 km E de Catemaco-Acayucán, *Gómez-Pompa 107* (MEXU). **Yucatán:** en los alrededores de la zona arqueológica de Sayil, 35 km SW de Oxtutzcab, *Cabrera 9041* (MEXU). NICARAGUA. **Zelaya:** Bluefields, 1 km W del poblado, *P. Moreno 24625* (MEXU). PANAMA. **Baru:** along ridge above Brazo Seco near Costa Rica border, *T. Croat 22561* (NY). VENEZUELA. **Trujillo:** Carr. Maracaibo–Agua Viva 16 km E de Agua Viva, *Bunting 5033* (NY).

2. *Thevetia amazonica* Duke, Arch. Jard. Bot. Rio de Janeiro 3: 247, pl. 16. 1922. TYPE: Brazil. Pará: Almeirin, *A. Duke 3058* (lectotype, designated here, MG not seen).

Shrubs 2.5–3.0 m. Laminae lanceolate, 10.0–13.0 × 1.0–1.8 cm, hirsute to tomentose. Inflorescences with 9 to 16 flowers; peduncles 0.6–1.8 cm, tomentose to glabrescent; bracts ovate, 4.9–7.0 × 3.0–4.3 mm, persistent, hirsutulous. Flowers with pedicels 2.3–

2.8 cm, glabrous; sepals ovate, 4.5–8.3 × 3.5–5.0 mm, hirsutulous; corolla yellow tinged with purple, hippocrateriform, tube 1.9–2.0 cm, 3.0–4.0 mm diam., internally glabrous, lobes oblong, 1.3–2.5 × 1.3–2.3 cm, extended; anthers 1.9–2.0 × 1.3 mm; ovary 1.3–1.7 × 1.5–1.7 mm, glabrous, style 0.7–1.0 cm, stigma 2.3 × 2.1 mm. Drupes 3.7–4.5 × 3.3–3.5 cm, lenticellate; seeds 2.4 × 1.2 cm, wingless, testa leathery.

Distribution. From Brazil to the north of Bolivia.

Discussion. *Thevetia amazonica* shares with *T. bicornuta* the tomentose indumentum and the wingless seeds with leathery testa, but *T. amazonica* is easily distinguished because it is the only species in the genus with lanceolate leaves and yellow corolla tinged with purple. In the original description, Duke listed four specimens, three of them from his own collections (3058, 3550, 4918) and the other from *Snethlage* 12455. Although we could not examine any of these specimens, we selected *Duke* 3058 as the lectotype following Gensel's (1969: 49) unpublished thesis, who mentioned that it is "the most representative and complete."

Selected specimens examined. BOLIVIA. **Departamento de Beni:** San Rafael, *Beck* 2664 (MO). BRAZIL. **Mato Grosso:** Mato Grosso, transpantaneire hwy., *Crawshaw* 284 (NY).

3. *Thevetia bicornuta* Müll. Arg., *Linnaea* 30: 392. 1859–1860. TYPE: s. loc., *H. A. Weddell* 3112 (holotype, P not seen).

Thevetia paraguayensis Britt. Ann. New York Acad. Sci. 7: 158. 1893. TYPE: [Paraguay.] Central Paraguay, *T. Morog* 381 (holotype, NY!; isotypes, GH not seen, MO!).

Shrubs 1.0–2.0 m. Laminae oblanceolate to spatulate, 5.0–12.0 × 1.5–4.0 cm, tomentose. Inflorescences with 10 to 15 flowers; peduncles 2.0–3.0 cm, tomentose; bracts ovate, 4.8–9.8 × 3.1–5.0 mm, persistent, hirsutulous. Flowers with pedicels 1.5–3.0 cm, tomentose; sepals ovate, 5.0–8.5 × 4.0–5.0 mm, tomentose; corolla yellow, funnelform, tube 3.0–6.0 mm, 2.0–4.0 mm diam., internally glabrous, throat 1.5–2.0 cm, 1.0–1.5 cm diam., lobes oblong, 2.0–3.5 × 1.5–1.7 cm; anthers 2.0 × 1.5 mm; ovary 1.5 × 1.5 mm, glabrous, style 3.0–4.0 cm, stigma 2.3 × 2.0 mm. Drupes 2.0–3.0 × 2.0–2.5 cm, not lenticellate; seeds 1.5–2.0 × 1.0 cm, wingless, testa leathery.

Distribution. From eastern Brazil to Argentina, mainly in the Chaco region.

Discussion. *Thevetia bicornuta* is easily recognized by the oblanceolate to spatulate leaf laminae and the funnelform corolla.

Selected specimens examined. ARGENTINA. **Formosa:** Estan. Bouvier, Riconada, *Guaglianone et al.* 468 (NY). BOLIVIA. **Santa Cruz:** Laguna Cáceres, swampy area set back from the channel of a stream or small river about 1 km W of the Río Sicuri, *Ritter* 4592 (MO). BRAZIL. **Mato Grosso do Sul:** Río Paraguai, porto Manga, *Hatschbach* 29551 (NY). PARAGUAY. **Alto Paraguay:** frente a Valle Mi, Riacho Mosquito, *Kiesling* 9702 (MEXU).